London School of Economics and Political Science

SOCIAL BONDING & NURTURE KINSHIP

compatibility between cultural and biological approaches

Maximilian Holland

First Edition published 2004 in the UK:

Senate House Library,
University of London,
Malet Street,
London WC1E 7HU

2012 Edition published internationally by Createspace Independent Publishing.
The current edition is essentially an unabridged version of the originally published doctoral thesis, reformatted, with typographical corrections, a new preface and index.

10 9 8 7 6 5 4 3 2 1

British Library Cataloguing Data

A catalogue record for this title is available from the British Library.

British Library Persistent ID: uk.bl.ethos.411642
Publication Type: Thesis (Ph.D.) - University of London, 2004.
Awarding Body: London School of Economics and Political Science
LSE Persistent ID: etheses.lse.ac.uk/465/

Holland, Maximilian P.
Social bonding and nurture kinship: compatibility between cultural and biological approaches / Maximilian P. Holland

Library of Congress subject classification: H Social Sciences > HM Sociology

352 pages. Includes table of contents, bibliographic references and index.
ISBN-13: 9781480182004
ISBN-10: 1480182001

SOCIAL BONDING & NURTURE KINSHIP

compatibility between cultural and biological approaches

PREFACE TO THE 2012 EDITION

This book contains the first widely available print edition of the doctoral thesis *Social bonding and nurture kinship*, completed at the London School of Economics and Political Science (LSE) in 2004. The thesis has previously existed solely in manuscript format in the LSE library archives, and has more recently become available in digital format from that same institution and also from the British library.

Why is this work only now available in book format? At the time, the thesis examiners (Elliott Sober and Christina Toren) were quick to suggest that it should be of considerable interest to scholars and academic publishers alike, with likely just a re-hash of the introduction and conclusion to broaden its appeal. But having successfully completed the research, and about to commence a teaching post, the last thing I felt like doing at the time was to immediately plunge back into rewriting two or more chapters. I wanted to let my hair down and have a change of mental scenery, and to enjoy the more tangible satisfactions of engaging students with ideas and critical enquiry, the potential for which had been one of my prime motivations in undertaking the PhD.

Another factor in putting the work to one side in 2004 was my disappointment with some of the levels of scholarship in the fields I had spent four years investigating. In retrospect, part of that disappointment was in fact with myself, for having fallen into an attraction to and engagement with certain areas of biological anthropology that appeared to promise a rigorous foundation upon which to understand the human condition. I had been exposed to the British educational system, with its training in the positivist tradition, trust in hard sciences, tendency towards reductionism, and neglect of the role of culture, relativism, and even modest aspects of postmodernism. Coming from this background, although there was the potential to engage with the latter ideas during undergraduate studies at the LSE, I was ignorant of their contribution and did not seek them out. Thus my initial attraction to and faith in the tools and frames of reference of areas of biological anthropology. For a young scholar there is of course also a great emotional appeal in a perspective that promises a rigorous and formal handle on a complex world, that makes it feel more predictable, and less threatening.

On a more conciliatory note I would maintain, both then and now, that a perspective on humans grounded in our ontogeny as part of the biological world is both well supported beyond the frailty of any single paradigm, perhaps logically unavoidable (it is hard to define 'human' for purposes of study without repeal to at least some biology) and increasingly urgent as we necessarily collectively re-examine our relationship with natural environments and our long term trajectory.

There are thus *a priori* reasons why rigorous insights from biology (if they can be arrived at) may enable a more nuanced understanding of the human condition. In practice however academic disciplines often suffer from training their members in a narrow tradition, suffer from cultural divisions, and compartmentalisation. These problems sometimes amplify into territorial disputes with other disciplines, mutual misunderstanding and sometimes mistrust, defensiveness and parochialism. Interdisciplinary scholarship, though much lauded, is seldom encouraged. The narrow disciplinary path, if unchecked, can lead towards dogmatism around methods, core assumptions (beliefs) and even data.

Having carefully worked through the theories and evidence around social behaviour and kinship during the research it has been hard to avoid the conclusion, then and now, that at least a small number of areas of biological anthropology (some parts of sociobiology and evolutionary psychology) may have suffered from these difficulties. That's not to say that some colleagues across the metaphorical corridor in cultural anthropology and other social sciences could not have more constructively engaged with the apparent gaps, though it is hard to do this when your entire body of data (ethnography) is disregarded and your approach is supposedly threatened with colonisation and reductionism! The current synthesis outlines a more constructive resolution.

What lessons might be drawn from this impasse and its eventual resolution? I would first look to narrow disciplinarity as the root of the problem. Then towards the general lack of awareness of the importance of culture (despite over a hundred years since Boas); both in how disciplinary culture affects our own openness as scientists (making potentially complimentary frameworks seem foreign and unwelcome); and especially in the human sciences, in how our inherited societal culture often constrains those of us tinkering with ideas about *human nature* to unwittingly derive our models from a culturally particular perspective which we then (and necessarily unsuccessfully) attempt to generalise to all humans. It is tempting to attribute these shortcomings to biologists, but note that cultural anthropologists themselves had only begun to deconstruct *their own* narrowly derived models of human kinship in the period between the late 1960s through the early 1980s (chapters 1, 3 and 8). In a historical sense then, it was this unfortunate timing that created the initial clash and subsequent impasse. Cultural anthropologists were changing their theoretical position on kinship around the time that biologists were starting to draw upon the kinship data that anthropologists had largely produced under the increasingly discredited 'old model'.

The work in this book inevitably had to wade through such debates, but precisely by engaging seriously with the theories and evidence of several approaches, it has produced a robust general framework for their resolution in this particular area of study (social bonding, social behaviour and kinship).

Readers will justifiably question how much of the original thesis remains valid and relevant in 2012, whilst research in the areas under study has not stood still. Two points should be made:

Firstly, the thesis builds its synthesis largely around the identification of a logical error common to sociobiological accounts, and supports this critique (and proposes a more parsimonious position) on the basis of both argument and wide ranging evidence. Here the fundamentals are unchanged. On the one hand, the same common error remains dominant in evolutionary psychology accounts; research continues to be regularly published which attempts to describe the extent to which the expression of human social behaviour is biased towards identifying and favouring genetic relatives, based on the mistaken assumption that this is a prediction of the fundamental biological theory. On the other hand, the broad pattern of the surrounding evidence drawn upon in the thesis has not been reversed by recent findings, just more detail added.

Secondly, debates around the robustness of *inclusive fitness theory* have arisen in recent years, specifically its relative parsimony compared to a *natural selection approach* as an accounting method for analysing multi-level selection. The language and framework of *inclusive fitness theory* forms the central thread of the biological account in the thesis (see mainly chapter 2), because this has long been the dominant theory and remains the *lingua franca* in biology. The thesis employs a broad definition of *inclusive fitness,* identifying the later developments of Price (1970), Hamilton (1975), Grafen (1985), Queller (1992) and Frank (1997) as being more accurate than Hamilton's commonly referenced 1960s papers. The thesis also deliberately distinguishes *inclusive fitness theory* from the narrower *kin selection theory* (cf. Hamilton 1975). In doing so, and in specifying the generality of *inclusive fitness theory* regarding levels of selection analysis, the thesis is largely neutral in respect of these recent debates. Further, an important aspect of the thesis is to remind us that a more primary necessary condition for the evolution of social behaviour is the *ecological potential* for grouping behaviours *before* considerations of genetic relatedness arise. This point is also made by Hamilton (1987) but rarely attended to in typical applications of the theory, which discrepancy provoked Nowak et al. to re-emphasise the point in their 2010 paper.

In short, I am confident that the contribution of the thesis to these debates over social behaviour remains undiminished, and trust that others may also gain from the insights contained herein.

Max Holland
October 2012

THESIS ABSTRACT

The current thesis aims to clarify some aspects of the relationship between biology and social bonds. The central task is to demonstrate that, despite clear problems of some past approaches claiming to represent biology, there is non-reductive compatibility between the perspective from cultural approaches documenting processes of social bonding in humans and the perspective from basic biological theory. In demonstrating this compatibility, the thesis also attempts to contribute to delineating the utility and limits of applying insights from biology to understanding aspects of human social behaviour, and to sociological study in general. The areas of social bonding and social relationships under focus are mainly at the level of individuals and primary social groups, rather than a structural-functional approach often employed in classical sociology of the family and comparative sociology.

The thesis initially reviews recent cultural approaches to understanding social bonding, and notes the potential academic value of a clarification of the association between social kinship and physical ('related by blood') kinship. In reviewing biological theory on social bonding and social behaviour, it is argued that classic sociobiological interpretations of this biological theory are erroneous in some crucial respects, and a different interpretation is argued for. Evidence on processes mediating social bonding in social mammals and particularly in primates is reviewed. It is demonstrated that circumstantial, social and contextual 'cues' typically mediate the formation of primary social bonds in these species, not genealogical relationship *per se*, and that these findings are compatible with basic biological theory. In the human case, it is demonstrated that the current interpretation of biological theory is also compatible with established disciplines closely associated with detailing mechanisms of social bonding (such as attachment theory). The consensus here is again that social bonds are mediated by various social and contextual cues rather than genealogical relationship *per se*.

Contemporary cultural approaches to describing processes of social bonding are investigated and found to be also compatible with the present interpretation of biological theory. With this basic compatibility

demonstrated, the possible implications for analyses of patterns of social bonding in human societies is discussed. Delineating the scope of the biological perspective underlines the importance of analysing sociological and cultural influences on patterns of social bonding, including historical, economic and political factors. This is illustrated with some examples.

CONTENTS

CHAPTER ONE – INTRODUCTION

1.1 THE ROLE OF THEORY

Greater understanding of the commonalities and distinctions between human cultures is as important a goal of academic research as ever; in particular, how changing local circumstances affect cultural practices. Disciplines most closely concerned with investigating and describing the variety of human cultures and their features have identified inherent problems in some previous concepts of 'human nature' (e.g. Schneider 1984) that mainly European and North American anthropologists and comparative sociologists have traditionally applied to other cultures. These kinds of problems have led to doubts about the validity of purportedly objective human 'universals' and thus a general move away from cross-cultural comparative study.

For these reasons, the place of theory in social science has become problematic. There is a tension between testing theoretical positions and avoiding potentially value-laden enquiry as Moore (1999) suggests;

> "…D'Andrade argues that any claim anthropology might have to moral authority 'rests on knowing *empirical* truths' (D'Andrade, 1995:402), and thus one should keep moral and objective models separate… [T]he purpose of an objective model is to gain a surer understanding of what is actually happening (D'Andrade, 1995:408). Other anthropologists decry this suggestion and point out that there is no such thing as value-free enquiry, and therefore it is impossible to keep moral and objective models separate. This debate is of course a version of an older debate…" (Moore 1999, 13, emphasis in original)

As Moore's review notes, the eschewing of theory on this basis now characterises much of anthropology. But she also points out that anthropology implicitly makes certain assumptions (about human *capacity* for meaning and culture) which are themselves theoretical in nature;

> "But, a theoretical claim that people everywhere have the capacity to create meaning and that this is a defining feature of human agency is based on a pre-theoretical commitment. This pre-theoretical commitment is of a very particular kind in the sense that it is ontological rather than

> epistemological: in other words, it implies something about the nature of being human that is believed to be universally true. The problem for anthropology is that in spite of the impact of post-modern theorising on the discipline and a political commitment to eschewing homogenizing and exclusionary meta-theories, the discipline still has to engage with theories that are about the commonalities – and not just the differences – between all human beings. The impetus for this is not just the dialogue that must exist between socio-cultural anthropology, biological anthropology, psychology, linguistics and other cognate endeavours in recognition of the fact that humans have biological capacities and an evolutionary history, but also the political and humanist project of recognizing and valorizing the fact that humans everywhere are human. For this to be the case, there must be something shared about being human." (Moore 1999, 17)

In the absence of this dialogue, there is a possibility that more biologically orientated disciplines (with perhaps a lack of social scientists' perspective on the actual diversity of human behaviours and practices) will attempt to advance hypotheses about human universals in the gaps left over by social scientists' methodological caution. Because these hypotheses derive from a tradition often less aware of cultural particulars, they in turn may again make the error of advancing a view of 'human nature' that derives mainly from within the practitioners' own cultures, whilst not recognizing the particularities of this view (see section 1.6 for examples). Meanwhile social scientists, particularly ethnographers, have compiled an unparalleled corpus of information about the actual range of human behaviour. I would therefore argue that, with this privileged position, the ability and responsibility lies with those familiar with this corpus to contribute to hypotheses about 'commonalities between all human beings'. Put differently, whilst the trend and desire for homogenizing meta-theories exists within academic life, social scientists must encourage reflexivity and ensure the premises of such theories are as 'objective' as possible.

1.2 THE TRADITIONAL CONNECTION: BIOLOGY, REPRODUCTION AND KINSHIP

I will argue that previous s*ociobiological* approaches to explaining human behaviour have not been compatible with ethnographic evidence because they both misinterpreted and misrepresented fundamental biological theory (see chapters 2 and 3). The main problems were; a particular *teleological* interpretation of the basic theory and; an agnosticism over the form of individual behaviour *per se* in favour of a focus on overall ('structural') social patterns. More importantly, anthropology through the 1960s and 1970s (culminating in Schneider 1984) identified a set of false, biologically-framed yet culturally-specific concepts about 'kinship' that had dogged the study of social relationships and interaction. These cultural conceptions, held both by anthropologists and by sociobiologists, included a focus on *relatedness by blood* (what the biologists called *genetic relatedness*) including purported local ideas of this. The long prominence of 'descent' models and their forebears exemplified this approach.

Some of the same assumptions that anthropology managed to identify and remove from its analysis *remain largely unidentified* by sociobiologists and others relying on hypotheses that they claim to be derived from basic biological theory. These include assumptions about the normalcy of the nuclear family and the universality of focus on males and related factors such as 'paternity certainty' and, most importantly, the supposed centrality of 'true' genetic connections in social relationships in humans.

Sociobiological hypotheses emerged at precisely the time (the mid 1970s) that anthropology was increasingly unburdening itself of these assumptions. This timing, and the fact that these hypotheses were not only incompatible with ethnographic data, but also overly simplistic, heavy handed and rode roughshod over many subtleties (e.g. Sahlins 1976), further alienated the mainstream of cultural anthropology from biology in general, and contributed to the current gulf between the approaches. The following two chapters will demonstrate how sociobiological hypotheses typically rely on a misinterpretation of basic biological theory. This section will review the anthropological perspective on the place of 'biology' in the study of social behaviour.

Schneider's 1984 *A Critique of the Study of Kinship* described in detail the problems with the anthropological study of kinship. In one way or another, anthropology had, since Morgan (1870), viewed social bonds and interaction in humans though the lens of 'kinship'. Schneider's critique deconstructed the concept and demonstrated that in utilising it, anthropology had uncritically conflated one the one hand, the study of social bonds and social behaviour and on the other, notions of biological (or 'blood') relatedness;

> "The purpose of this book is to make explicit and examine carefully the implicit and explicit assumptions and presuppositions about kinship, and to evaluate them carefully." (Schneider 1984, 39)
>
> "There is general agreement that there is such a thing as "kin-based society," though just exactly how this is defined may vary from scholar to scholar. With a few exceptions there seems to be general agreement that an important aspect of the definition of kinship is its entailment in biological and/or social reproduction." (Schneider 1984, 43)
>
> "For Radcliffe-Brown, as for Maine and Morgan before him, "the chief source of social cohesion is the recognition of kinship" (Radcliffe Brown 1950:43)… There may be a further corollary here in some views that is lacking in others – that there is a quality, which is both social and biological, to kinship which gives it its special force. Certainly for Morgan (1870:10) the actual bonds of blood relationship had a force and vitality of their own quite apart from any social overlay which they may also have acquired, and it is this biological relationship itself which accounts for what Radcliffe-Brown called "the source of social cohesion."" (Schneider 1984, 49)

This underlying reference to the concept of *bonds of blood*, established by Morgan, had continued (through Radcliffe-Brown and others) up to the time of Schneider's writing. However, there were incompatibilities between this notion and the ethnographic evidence. For example, from before Morgan, it was acknowledged that, even in the case of the closest social ties, bonds of blood are not in fact necessary (Maine 1861, on the 'legal fiction' of *adoption*, see Schneider below). Mounting ethnographic evidence later demonstrated these incompatibilities clearly. For example, what Euro-American culture has traditionally designated as *adoption* may not be distinguished by many cultures, nor even applicable. In some Inuit societies, anywhere between 25 to 70 percent of children may live away from blood parents in an 'adoptive' social arrangement (Guemple 1979, see also Brady 1976, Terrell & Modell 1994 and chapter 8). Partly because such cultures do not mark an 'adoption' concept as such, the high frequency of 'non-blood' primary social bonds has often gone underemphasized, and underreported in ethnographic summaries (Goody 1969). An ignorance of such realities caught out sociobiologists in their attempts to explain human social patterns (Sahlins 1976). When one sociobiologist later took a closer look at Inuit culture, she had to concede that theory clashed with the evidence;

> "It is also clear that some of the elements of Inuit adoption are difficult to explain from an evolutionary perspective. For example, parents do not always bias investment in favor of their own offspring. Spencer (1959) describes a woman who risks her life and the life of her unborn child in order to avoid abandoning her adopted son. Guemple (1979) also remarks on the fact that adopted infants sometimes receive better treatment than natural children. Some of the motives that prompt people to adopt are also difficult to explain. In some cases, affection for children appears to provide a sufficient motive to adopt. Other individuals adopt a large number of children as a means of establishing prestige or status. Even if such cases are not common, they suggest that evolutionary principles may account for only some of the observed variation in adoptive behaviour."
> (Silk 1987, 328)

The point about adoption is that it clearly demonstrates that social bonds are constructed, and that this may in fact be independent of genealogical relatedness. Schneider himself emphasised a distinction between the notion of a social relationship as intrinsically 'given' and inalienable ('from birth'), and a social relationship as created, constituted and maintained by a process of interaction, or 'doing' (Schneider 1984, 165). Schneider used the example of the *citamangen* / *fak* relationship in Yap society, that he himself had previously glossed over as a 'father / son' relationship, to illustrate the problem;

> "The crucial point is this: in the relationship between *citamangen* and *fak* the stress in the definition of the relationship is more on *doing* than on *being*. That is, it is more what the *citamangen* does for *fak* and what *fak* does for *citamangen* that makes or constitutes the relationship. This is demonstrated, first, in the ability to terminate absolutely the relationship where there is a failure in the doing, when the *fak* fails to do what he is supposed to do; and second, in the reversal of terms so that the old, dependent man becomes *fak*, to the young man, *tam*.
>
> The European and the anthropological notion of consanguinity, of blood relationship and descent, rest on precisely the opposite kind of value. It rests more on the state of *being*, on the sharing of certain inherent and therefore inalienable attributes, on the biogenetic relationship which is

> represented by one or another variant of the symbol of "blood" (consanguinity), or on "birth," on qualities rather than on performance. We have tried to impose this definition of a kind of relation on all peoples, insisting that kinship consists in relations of consanguinity and that kinship as consanguinity is a universal condition. The genealogical grid of consanguineal relations is regarded as a universal statement of relations of substance, more generally, of *being,* of inherent quality, while performance, forms of doing, various codes for conduct, different roles, are seen as variables, secondary, attached as different possible meanings to the fundamental set of signs which the genealogical grid, as relations of being or substance, represent." (Schneider 1984, 72)

This distinction between 'being' a blood (or 'genetic') relation *per se* and the significance of the process or performance which makes the relationship has been one of the central concepts of kinship studies since Schneider, and finds a parallel in the current thesis. The following sections will illustrate more detail of Schneider's argument. It is also worth noting how those subsequently working in the area of kinship have themselves interpreted Schneider's impact;

> "The crux of Schneider's (1984) argument was that anthropologists had founded the domain of "kinship" on the notions of human reproduction and the biologically defined relatedness of their own Euro-American culture. Human reproduction and notions of biological relatedness cannot be presumed to elsewhere structure people's social relationships, and Schneider himself very clearly doubted that they do so. His criticism was sweeping, covering not only anthropologists who, like Scheffler (1973), explicitly referred to human reproduction in their definitions of kinship, but to all anthropologists, who, since Morgan, explicitly or implicitly grounded kinship in biological relations even when they described cases of "kinship" locally formulated in some other terms. Schneider concluded that "kinship" as conceived in anthropology could not be meaningfully studied cross-culturally." (Galvin 2001, 110)

Schneider's critique is widely acknowledged to have marked a turning point in anthropology's study of social relationships and interactions (Collier and Yanagisako 1987; Carsten 1991, 1995, 2000; M. Strathern 1992; Holy 1996; Schweitzer 2000). The undefined label or domain formerly known as 'kinship' has largely been avoided ever since.

Notice that Schneider's critique uses 'biological' mainly to refer to the *concepts* of procreation and 'blood' relatedness;

> "However it was figured, the reproductive relationship was taken as the central feature of kinship. Kinsmen, then, were those who were related through "real" biological ties… For Morgan kinship consisted in the knowledge of the existence of relationships of human reproduction. Before the facts of reproduction were known there could be no kinship… The major modification was in the shift of emphasis from the social recognition of biological bonds arising out of procreation to the sociocultural aspects themselves, ostensibly giving the real or putative existence of the ties lesser, if any importance… But the concept of adoption demonstrates that the ultimate reference remained biological. That is, it is the sociocultural attribution of meaning to the biological relationship (real or putative) which is the central conception of kinship. Without the biological relationship there is nothing. Indeed, without the biological relation it is called "fictive kinship," presumably following Maine (1861:27), who argued that where no actual biological relationship exists it can be treated as if it does by a legal fiction, as in adoption. This is only another way of bringing in the biological facts…" (Schneider 1984, 54)

Schneider's argument is persuasive. However, his critique of the biological referent to social bonding needs to be clearly understood as a critique of these pseudo-biological concepts, and not a critique of biology (as scientific study) itself (see also Feinberg 2001). Schneider was not claiming that genetic relationships between individuals do not exist, he was questioning their cultural value and questioning the basis of claims of their necessary connection to actual social relationships;

> "It is possible, even probable, that the facts of genetic relationship, like colour, are the same the world over and can be defined in precise, scientifically established terms. Different degrees of genetic relationship can be specified with respect to ascendants and descendants. In this respect, a genealogy which is in fact a statement of genetic relationship, or even a statement that has a high likelihood of being as close to the real genetic relations as possible, can be regarded as equivalent to the wavelengths that define the colour spectrum. But Barnes in 1964 made it perfectly clear, if it had not been perfectly clear before, that there was a radical difference between genetic relations as defined by the criteria of

> “science” and what are culturally regarded as kinship systems.” (Schneider 1984, 124-125)

He also makes this distinction elsewhere;

> “I have said that the American ‘kinship’ system has two distinctive features, shared biogenetic substance and diffuse, enduring solidarity. I have said elsewhere that these derive from the master symbol of coitus and that each is a facet of this act. The last few pages of my book, *American Kinship*, make the point that the biological elements have a symbolic significance. They constitute an integrated set of symbols in the sense that they are a model for how life, in certain of its aspects, is constituted and should be lived. The symbols are ‘biological’ in the sense that the culturally given definition of the symbol system is that it is derived from the facts of biology as a process of nature itself. But it is fundamental to our understanding that we appreciate that these biological elements are symbols and that their symbolic referents are not biology as a natural process at all. [Schneider here adds in a note] It is even a moot question as to whether the symbols derive from the facts of nature and the facts of biology as these can be determined scientifically. What is indisputable is that the symbols are formed of elements which in native culture are defined as biological, particularly as aspects of the reproductive process. What is disputable is whether they in fact derive from, or mirror, or are models formed after the scientific facts of biology. I do not think that they are, but this subject is best left to another time.” (Schneider 1972, 45, 62)

> “I stress that the genealogical relationship must be culturally “recognized” or culturally constituted, for it is hard to see how it could serve as a language or idiom if it were not given clear cultural formulation. We believe that all mammals have real biological relationships which can be stated in genealogical form. But where such biological relationships are given no social or cultural value whatsoever, or are treated as irrelevant or non existent, or are not recognized to exist, it is hard to see how they could be treated as a language of any sort.” (Schneider 1984, 62)

One of Schneider’s main concerns was that *justification* for the (supposedly universal) privileging of the procreative ‘blood’ relationship in social ties was never actually given by kinship theorists, although their concept of ‘kinship’ frequently made reference to ‘biology’ and ‘natural facts’. This point is made repeatedly in his *Critique*;

> “Let me put the problem in a different way. Of all of the imaginable and of all the well-known features of folk-cultural theories of reproduction, what reason do Scheffler and Lounsbury have for insisting that kinship relations are those predicated on birth and on the relation between sexual intercourse and reproduction and further have the character of indissolubility? Scheffler and Lounsbury offer neither explanation nor rationale for these three remarkable a priori conditions of their definition. In fact, they are simply bringing *our* biology (I do not mean genetics) back into what is presumed to be *their* (the natives’) cultural theory of reproduction, and so they restore the Morganian definition.” (Schneider 1984, 118)

> “Is kinship a privileged system? Does its special privilege reside in its roots in biology or sexual reproduction? If so, just how? Spiro answers none of these questions for us. Neither does Malinowski.” (Schneider 1984, 139)

> “The privileged position of kinship has been argued by functionalists of many particular persuasions, from Malinowski through Talcott Parsons, as one which is based on its vital functions. In the absence of a clear and compelling demonstration of precisely what those vital functions are and how they determine or constrain specific cultural forms, functionalism must be dismissed as failing to resolve that issue. The question of whether kinship is a privileged system and if so, why, remains without a satisfactory answer. If it is privileged because of its relationship to the functional prerequisites imposed by the nature of physical kinship, this remains to be spelled out in even the most elementary detail.” (Schneider 1984, 163)

Schneider demonstrated clearly that no convincing justification had been made in reference to biological ‘constraints’ (he included the sociobiological position, since it too didn’t fit the ethnographic evidence, see above). Notice that, despite common interpretations (see for example, Galvin 2001, above) Schneider was not saying that comparative study of ‘kinship’ (as social ties) is impossible (Feinberg 2001), just that the genealogical element intrinsic to the established concept of ‘kinship’ must be removed;

> "The matter is quite simple. Given the definition of kinship as genealogy, by definition genealogy has priority over related phenomena. If this definition proves inadequate to the study of some societies, then we are forced to three alternatives. We can exclude the societies to which the definition of kinship does not apply, we can change the definition of kinship, or we can abandon the whole notion of kinship. But we cannot smuggle in new criteria by which kinship is defined, such as sharing land or altruism, and still think we are dealing with kinship as genealogical or biological relatedness." (Schneider 1984, 131)

Schneider's references to sharing land and altruism will become clearer in later chapters (chapters 8 and 7, respectively). As well as not denying the possibility of comparative study, and neither criticising biology as a discipline, Schneider was also "explicitly *not* speaking of "kinship" at a psychological level" (Schneider 1972, 39). This has left open the option for ethnographers to investigate the psychological processes involved in social bonding, and such perspectives are more common that they used to be (cf. Carsten 2000, see section 1.7), as later chapters will illustrate.

The present research is intended to demonstrate that *cultural approaches* to 'kinship' are not only compatible with "the scientific facts of biology" (as Schneider himself suggested they should be), but also that such ethnographic data is vital for the (empirically narrow) biological and psychological perspectives on human social and emotional bonding processes.

Assumptions about the necessary significance of genetic relatedness that dogged former approaches (in both anthropology and sociobiology) are not accurate in their claims to be "models formed after the scientific facts of biology" (again, as Schneider believed). The current interpretation of the biological position instead emphasises a continuity with psychological mechanisms that mediate social bonding, in particular, 'attachment' mechanisms. Past interpretations of 'biological facts' have often suggested that 'biological forces' are pervasive and omnipresent (giving rise to the charge of biological determinism), and that, at some level, all human behaviour can be understood as the means to a 'biological goal'. The current approach thoroughly rejects any such teleological claims; biological processes have no 'goals'. This approach therefore emphasises that, in human societies, “the biological facts are… but one of the conditions, like ecology, [political] economy, demography etc., to which kinship systems must adapt.” (Schneider 1984, 139, see chapter 9 for discussion).

1.3 HISTORICAL ASPECTS OF SOCIAL SCIENCES’ RELATIONSHIP WITH BIOLOGY

1.3.1 SOCIAL DARWINISM AND RACE THEORY

In this section I will discuss some other aspects of anthropology’s relationship with biology, but this can in no way be a thorough review. I focus mainly on those areas relevant to the current focus on kinship and social bonding.

We have seen (above) that much of the study of social relationships was from the start approached via the framework of biological relatedness. But biology’s relationship with early social science covered more than just kinship. Prior to Boas (1911), cultural variations between societies were usually ascribed to purported different innate (‘biological’) potentials. Added to this, the notion of progressive ‘social evolution’ from a ‘primitive’ promiscuous state to a ‘civilised’ one was also popular, providing, for example, the reasoning for Morgan’s focus on an analysis of ‘classificatory’ versus ‘descriptive’ kinship terminology.

The supporters of strong ‘social evolution’ theories attempted to give them justification, credibility and respectability by suggesting that they were derived from an increasingly influential theory of a mechanism of *biological* evolution (Darwin 1859). However, as ‘social evolution’ and ‘Social Darwinism’ ideas gained momentum, Darwin and others who were involved with the biological work clearly stated that their own ideas about ‘natural selection’ were properly understood to be applicable only to biological forms, that is, the physiological and behavioural characteristics of organisms, and explicitly not to human societies and cultures through notions of human ‘social evolution’. More importantly, the derivation of any ‘moral values’ modelled on the (blind and inherently amoral) process of biological evolution was strongly warned against (Huxley 1893, see below).

Yet these warnings went unheeded by contemporary social evolution theorists, such as Herbert Spencer.

Spencer's ideas, perhaps sometimes now taken out of context (Sahlins 1960), were well received in an explicitly imperialistic age when members of some societies had a vested interest in justifying interference in and often exploitation of other societies and their resources. Using an influential natural scientific theory (Darwin's theory of the evolution of biological species by natural selection) as a political and moral justification for some human groups to dominate others was a sleight of hand which went far beyond descriptive natural science. This attempted extrapolation from the 'fact' of biological evolution to a political/moral position was, and remains an instance of the 'naturalistic fallacy', in this case, seeking to base morality and value on a blind and mindless material process (what Huxley, below, calls the 'cosmic process'). As well as the same caution about conflating 'fact' and 'value' being given by Moore (see above), maintaining this distinction has long been the position of many biologists. Perhaps most notably, T. H. Huxley ('Darwin's Bulldog' and colleague) was provoked to express his views precisely by the rise of Spencer's 'Social Darwinism';

> "Social progress [as a humanist project] means a checking of the cosmic process at every step and the substitution for it of another, which may be called the ethical process... it requires that the individual should not merely respect, but shall help his fellows. It repudiates the gladiatorial theory of existence... Let us understand, once and for all, that the ethical progress of society depends, not on imitating the cosmic process, still less in running away from it, but in combating it." (Huxley 1893)

Huxley, though methodologically sceptical about natural selection (Lyons 1999), was a close colleague and friend of Darwin, whose theory was a considerable contribution to illuminating the workings of the 'cosmic' process and exposing its amorality. Not surprisingly, to medically inclined evolutionary biologists, natural selection in its 'blindness', should be seen as a force to be wary of, or put another way; 'Mother Nature is a wicked old witch' (Williams 1993). But 'Social Darwinism' essentially modelled morality on this mindless process.

Around the same time, 'race theory' similarly made claims to scientific objectivity, by making reference to the new theories of biological evolution. These unwarranted claims of a direct association with Darwin's work in turn sometimes gave the latter a bad name, such that the two are still today often believed to be somehow connected;

> "The race theory *was firmly anchored in the new science of biology* by evolutionary ideas which suggested that some races were more primitive than others, and therefore more animal-like, or 'theriomorphic', in bodily form, mental ability, and moral development. The theory measured each race against the supposedly more advanced, the northern Europeans." (Carrithers 1996, 394, emphasis added)

From the full content of his review, it is clear that Carrithers has a subtle understanding of the current biological position. The point is that it is quite easy, when looking at the history of social science, to perceive a picture of *biology itself* as inevitably promoting notions of e.g. racial differences or fixed genetic potentialities, as well as a downplaying of developmental / environmental / social / cultural factors on behaviour. This was never an accurate portrayal of core biological theory, and better reflects cultural values justified in vague reference to 'biology' (e.g. Schneider 1968, and above). Today the biological position is clear enough;

> "We now have a vast array of molecular data which speaks so eloquently towards our recent African origin within the last 200,000 years or so. This African origin was followed by approximately 100,000 years of further diversification within Africa, followed by subsequent migrations and dispersals throughout the rest of the world within the last 100,000 years. Such a shallow history precludes the creation of biologically based racial typologies. It similarly forestalls claims of deeply rooted biological differences between populations. Rather than recoiling from the study of biological variation, anthropologists and other scientists should widely disseminate the results of their studies. Such data clearly refute folk theories of the differences between peoples and clearly demonstrate the unity of humankind." (Disotell 2000, 23-24)

It was against the contemporary intellectual climate in which 'race theory' and 'Social Darwinism' were prominent, and proclaimed by advocates as 'scientific', that Boas advanced a different perspective;

> "Boas broke the evidently seamless simplicity of this theory… He argued that there is no reason to think that other 'races' (or, more accurately, other ways of life) are less moral or less intelligent than northern Europeans, and so there is no single standard for evaluation… [F]ield research would reveal forms and patterns in human life… so various, he argued, that they could not have arisen from a uniform process of social or cultural evolution but must rather be the fruit of complex local historical causes." (Carrithers 1996, 394)

These ideas were introduced by Boas in his *The Mind of Primitive Man* in 1911, and further developed by his equally influential students, including Sapir, Benedict, Kroeber, Mead (and through the latter and Kluckhohn, handed on to the likes of Schneider, see e.g. Schneider and Handler 1995). These anthropologists empirically demonstrated the great plasticity of human behaviour.

1.3.2 BIOLOGY, GENDER, ROLES

Another trend in early comparative sociology (e.g. Westermarck 1891) was the attempt to define an 'essential form' of the human family, assumed to be fundamental and universal, which employed notions of what kinds of arrangements are 'natural'. Such discussions in turn often invoked 'parental roles' which were defined according to the sex of parent. Assuming a state of 'primitive promiscuity' where paternity was indeterminable, the rise of the nuclear family had been tied to the development of monogamous marriage (Morgan 1877, Engels 1884). Amongst others, Malinowski (1913) suggested a distinction between social and physical 'kinship'; whereas the bond between an infant and its 'mother' is usually physical as well as social, he suggested, the role of the father is essentially social, and may or may not be physical.

As Schneider pointed out (see above), later functionalists followed this distinction between the roles of the mother and father, and regarded the mother-child dyad (or 'matricentral cell') as 'natural' and given. The 'given-ness' of the 'maternal' bond – arising from the high frequency of the correlation between what could, after examination, be deconstructed into 'child's social and emotional bonding figures' and 'the female having given birth' was not adequately examined. Although some later functionalists (e.g. Spiro 1977) noted this distinction (Schneider 1984, 138-139) in general few of the features (psychological, interactional) of the 'matricentral cell' were closely investigated within anthropology (e.g. Carsten 2000, and see chapters 8 and 9). The investigation of this aspect of the supposedly 'natural' was taken up psychologists and attachment theorists (e.g. Bowlby 1969), and the growth of knowledge in this area was taken up by a later generation of anthropologists precisely to question the notion of the *natural* 'matricentral cell'.

For Fortes (1959), the naturalness of the mother-offspring relationship was at the heart of his distinction between the 'female' domestic domain and the male political domain. This conception of the natural roles of males and females (and the simple model of domestic/public spheres) has since been heavily criticised. Fortes' position has been taken as an example of a deep gender bias in anthropology, and some aspects of the purported 'naturalness' of sex-roles and male-female bonds (e.g. female dependence on male hunting) have been challenged using data from primatological studies and biological theory. I here review some of the ways in which the *status quo* regarding the given-ness of 'natural' gender roles and related categories, and especially the explanatory focus on males, have been questioned by anthropologists by invoking biological data (typically evidence from other primates). Initially, such biological 'facts' were used to cast doubt on some dominant assumptions about what is 'natural' or 'given'. Later, however, some (Yanagisako and Collier 1987) questioned this whole focus on ideas of what might or might not be 'natural' since an emphasis on historical/evolutionary referents itself seemed to reinforce an impression of 'natural' *constraints*. The following sections illustrate this move through primate data to a non-biology-invoking position.

Slocum (1971) pointed out the male bias in anthropology; "Anthropology, as an academic discipline has been developed primarily by white western males, during a specific period in history." (Slocum 1975 [1971], 37). She goes on;

> "There is a strong male bias in the questions asked, and in the interpretations given. This bias has hindered the full development of

> anthropology as "the study of the human animal"… I am going to demonstrate the Western male bias by re-examining the matter of evolution of Homo sapiens from our nonhuman primate ancestors. In particular the concept of "Man the Hunter"… Hunting cannot explain its own origin. It is much more logical to assume that as the period of infant dependency began to lengthen, *the mothers would begin to increase the scope of their gathering to provide food for their still dependent infants.* The already strong primate mother-infant bond would begin to extend over a longer time period, increasing the depth and scope of social relationships, and giving rise to the first sharing of food. It is an example of male bias to picture these females with young as totally or even mainly dependent on males for food. Among modern hunter-gatherers, even in the marginal environments where most live, the females can usually gather enough to support themselves and their families." (Slocum 1975 [1971], 37-43, emphasis in original)

Slocum's point is that, in the reconstruction of human evolution, "male bias exists not only in the ways in which the scanty data are interpreted, but in the very language used" (Slocum 1975 [1971], 38). She puts forward an equally plausible suggestion, supported by primate evidence available at the time, focusing on females and their social bonds with their offspring. At the same time, Kathleen Gough (1975 [1971]) also used primate data and that from hunter-gatherer groups to question some assumptions about the origins of the family and the relationship between sedentary agriculture and monogamous arrangements. Like Slocum, she suggests that;

> "All primates share characteristics without which the family could not have developed… Childhood is longer, the closer the species are to humans. [In Chimpanzees] the long childhood and maternal care produce close relations between children of the same mother, who play together and help tend their juniors until they grow up." (Gough 1975 [1971], 55)

Adrienne Zihlman (1981) makes similar points about the male-bias in anthropology as well as in theories of human evolution. Thus, as well as charging those promoting the concept of "man the hunter" (e.g. Lee and DeVore 1968), she similarly criticises sociobiological theories in respect to their claim to explain aspects of human evolution, for their similar male-bias;

> "[A]t the same time, Wilson's *Sociobiology* uncritically emphasizes male dominance, male fitness and male reproductive success… The concepts of parental investment and mate choice, pillars on which sociobiology is founded, are never in this book applied to female mammals or primates. Though Wilson mentions that maternal care is prolonged in higher primates and humans, and that social relationships are to some extent matrilineal, these facts play no essential role in his theoretical formulation of human societies today or yesterday. The intellectual tradition of Wilson's emphasis on male reproductive success appears as a barrier… for incorporating women into human evolution." (Zihlman 1981, 84)

The assumptions and biases of biologically based analyses will be investigated more fully below (chapter 3), and the role of such biases in obscuring productive insights discussed. Like Gough, Zihlman (1993) draws on primate data on female-offspring relationships, particularly noting the frequent occurrence of food-sharing within such relationships in Chimpanzee groups, especially compared to the low frequency of food provision by males. Since these studies, further primate data has become available, sometimes lending support, sometimes raising further questions about such analyses. The point to note here is that social scientists have at times successfully used biological data to support arguments that question some of social science's own (as well as biology's) long-standing narrow assumptions.

Later theorists have adopted a more cautious approach, and have suggested that any appeal to biological data or analytical categories, e.g. of child rearing/the domestic domain versus the public domain, may simply reveal "our tendency to rediscover gendered dichotomies" (Yanagisako and Collier 1987, 49). They suggest that the feminist perspective first challenged male-bias in anthropology (as above), then questioned whether male-dominance was indeed a cross-cultural universal, and rejected it as a 'natural fact' and redefined it as a social fact (*ibid.*, 14). Yanagisako and Collier's innovation was to suggest that the (cultural) categories of 'male' and 'female' and the social and cultural processes by which they are constituted should themselves be investigated. Though they do not doubt that men and women are different (*ibid.*, 48), they thus emphasise the value of cultural analysis to help discover the lenses through which these categories, concepts and symbols are constructed. In this respect, Schneider's various critiques of the cultural values inherent in the concept of 'kinship' were an important influence;

> "Just as Schneider (1968) questioned, rather than took for granted, the meanings of blood, love and sexual intercourse in American kinship and their influence on the construction of categories of relatives, so we have to question the meanings of genes, love, sexual intercourse, power, independence, and whatever else plays in to the symbolic construction of categories of people in any particular society." (Yanagisako & Collier 1987, 41)

Yanagisako and Collier's questioning of the social use and cultural meaning of these categories can also be supported by "scientific facts of biology", which demonstrate that a simple and clear division between two discrete sexes is not always present (see e.g. Cucciare 1981 for an early review). Biological facts can thus themselves be employed to re-examine the extent to which purported biological dispositions are really 'given' rather than socially and culturally constructed. Thus, whilst Yanagisako and Collier acknowledge male and female differences, they call for a consideration of how these differences are understood and *misunderstood* and used (and *misused)* in the cultural construction of gender categories. They reject an insistence on the 'naturalness' and possibly therefore 'rightness' of the social/cultural roles associated with biological differences. Huxley (above) had this very distinction in mind when he criticised Social Darwinism; questioning the institutionalisation of social categories and associated prescriptive moralities based on unexamined 'natural facts'.

As an example of this which is relevant to the current research, and to Schneider's points about kinship (above), recent work examining varieties of caregiving to dependent infants and children demonstrates the flexibility of what are usually taken to be fairly fundamental aspects of 'natural' roles. While an extended developmental period and reliance on caregivers may perhaps be a 'biological need' of the dependent infant; the corresponding role of caregiver(s) need not be fulfilled by any particular sex of nurturer (Geiger 1996). It could be argued that the traditional Euro-American cultural category of 'the role of the mother' as sole primary caregiver derives from a combination of; on the one hand these (relatively inflexible) needs of the infant; and on the other the (culturally specific) social structure and typically isolated living arrangements of individuals and nuclear families. Research in other cultures (Tronick et al. 1985, see chapters 7 and 8) suggests that the Euro-American pattern of a single (and often female) caregiver is only one out of many possible arrangements. A superficial cultural interpretation of the 'natural facts' can thus suggest a great deal more rigid picture of dispositions and processes than emerges from a clear investigation of the *actual* biological facts (as Schneider suggested).

1.4 DECONSTRUCTING 'KINSHIP'; GENEALOGY OR SOCIAL BONDS?

The main focus of the current research is on social bonding behaviours, and the commonalities between the ethnographic evidence and the (basic and correctly interpreted) biological position regarding these behaviours. This section and the following will very briefly illustrate how anthropological studies of social behaviour have progressed since the assumptions that were intrinsic to 'kinship' were identified (see section 1.2 above). Although this work will be reviewed and discussed more fully later (chapters 8 and 9), what emerges from this quick review is that the study of social ties is alive and well. As mentioned above, Schneider has successfully shown that the concept of 'kinship' had been a conflation of what should properly be two separate concepts, 'social bonds' and 'biological relatedness'. Future analysis would thus have to consider these two factors independently (if at all). Anthropologists of different inclinations have recently emphasised one or other of these two components that made up the old notion of 'kinship', and in a sense, each emphasising their continuity (albeit having incorporated Schneider's critique) with anthropological tradition and ethnographic data;

> "For Schneider (1984:200-201) the central question is: Given our definition of kinship, do other people have it, and what value and meaning do they give to it? I would suggest, by contrast, that the central question should be: how do the people we study define and construct their notions of relatedness and what values and meaning do they give them? It seems to me that we would do better to use the term "kinship" to characterise the relatedness that people act and feel. In this way we may

> arrive at a new and much more flexible approach to the study of kinship in anthropology." (Carsten 1995, 236)

This recasting the phenomena to be studied as 'relatedness' was later criticised as too broad a target as to be useful since, on its own;

> "[T]he concept of relatedness does not specify what precisely 'relatedness' is meant to involve, how it is to be defined and how it should be distinguished from any other kind of social relationship… to avoid equating the concept of relatedness with any kind of social relationship ['friends, neighbours, citizens, fellow-worshipers, producers and consumers, members of the same ethnic group'], those who advocate its usefulness restrict it to relationships which resemble those of traditionally defined kinship. Replacing the concept of kinship with that of relatedness thus amounts in practice to a semantic solution to the difficulties involved in the definition of kinship. But renaming a phenomenon does not solve the problems involved in its conceptualisation." (Holy 1996, 168)

Holy's critique of Carsten's shifting the discussion to 'relatedness' echoes Schneider's critique of the concept of 'relationship system' (Schneider 1984, 111) as used by Needham (1971) and Maybury-Lewis (1965). As Holy makes clear, he instead favours a position which maintains the traditional guiding principle of shared substance ('consubstantiation') to explain the social connections ('relatedness') between people;

> "The current debate about how kinship should be conceptualised and defined has made it abundantly clear that in many cultures the system of relationships, which resemble what we would commonsensically call 'kinship', is not necessarily based on the tracing of genealogical connections. What the debate about the culturally specific extra-genealogical conceptualisations of kinship seems not to have sufficiently appreciated is that genealogical relations, which are central to the traditional anthropological definition of kinship, are a specific Western way of imagining relatedness among people resulting from their sharing of substance and its transmission over generations… [T]o be meaningful as a concept, kinship has to be understood as a culturally specific notion of relatedness deriving from shared bodily and/or spiritual substance and its transmission." (Holy 1996, 170-171)

If the concept of 'kinship' was, as Schneider suggested, a conflation of 'biological relatedness' and 'significant social bonds and interactions' there would seem to be two elements that one might wish to investigate (independently of each other). For Holy, the connectedness-by-consubstantiation (of which the Euro-American 'genealogical relatedness' is one cultural form) remains of interest and he suggests that this is the 'universal' concept which deserves preserving.

On the other hand the alternative emphasis that Holy ascribes to Carsten (1995) and Bouquet (1993) of 'relatedness' is as a concept that 'does not presuppose that genealogical relations are necessarily the most important' (Bouquet 1993, 157), but which does give a sense of the focus on social bonds and interactions. Of course, in having this emphasis, as Holy points out, and Carsten (2000) concedes, this conversely has the weakness of not delineating which category of 'relationships' are considered significant. But, having suggested that the two elements that made 'kinship' should in fact not be conflated, unless one entirely recasts the way that these two supposedly universal aspects are in fact correlated/covariant (or not), one must keep the two elements separate.

At the same time, it seems that Holy's notion is not really a move away from the 'genealogical view' critiqued by Schneider. He suggests that each society will create a set of conditions by which individuals consider themselves related through sharing substance, and consider their essence to be transmitted between the generations. However, where the concepts of substance and consubstantiation do appear in ethnographies, they typically do not signify inalienable 'being'; on the contrary they involve the individual's continuous *transformation* throughout the life span by coming into contact with ever changing influences in the environment (e.g. Ingold 2000, Storrie 2003, see chapter 8). This use is very different from the eternal, down-the-generations 'consubstantiation' as used in the "Western way of imagining relatedness". Because of such ambiguities, some theorists have suggested that the concept may not be a helpful one (e.g. Thomas 1999, Carsten 2000). In sum, in maintaining the emphasis on "the state of *being*, on the sharing of certain inherent and therefore inalienable attributes… on qualities rather than on performance" (Schneider 1984, 72), Holy's position appears to ignore the essence of Schneider's critique.

1.5 A CONTINUING APPEAL TO 'NATURAL FACTS' BY SOCIAL SCIENTISTS

Not everyone accepted all elements of Schneider's critiques. Some of those whose use of 'kinship' he criticised have nevertheless continued essentially along the same lines as before (e.g. Scheffler 2001, Goodenough 2001). In a recent review of the history of the study of kinship, in the introduction to his recent edited volume, Schweitzer concludes by emphasising the need for more dialogue between cultural and 'biological' approaches;

> "I believe that the issue of the relationship between kinship and biology still awaits a balanced answer. While the last twenty years were characterised by extreme positions – with the complete decoupling of kinship and biology by culturalist and feminist approaches, on the one hand, and the reduction of everything to biology by sociobiology, on the other hand – none of these positions is entirely satisfying. After all, while it has become evident that biology alone is insufficient for a comprehensive understanding of what kinship *is* and *does*, it is equally hard to maintain that kinship has nothing to do with biology and procreation." (Schweitzer 2000, 16)

However, Schneider's point was not that 'kinship' has nothing to do with biology and procreation (see above). His point was that it is not enough to make vague appeal to biology and procreation, 'kinship' theorists must *justify this proposition* (if indeed it could be justified); just what exactly does 'kinship' have to do with biology and procreation? If theorists cannot advance a model for this connection, and can neither demonstrate that a culture under study explicitly values biological (or 'folk biological') aspects, there can be no basis for the claim that their bonds form 'because of the natural facts'.

Goodenough (2001) included a discussion of the 'natural basis' of kinship ties, appealing to the notion that; "As a group, a mother and her children constitute a natural isolate in a human community as against other such mother-child groups. As the members of such a group look primarily to one another for mutual support, emotional bonds develop among them" (Goodenough 2001, 206). Whilst this account perhaps gives more detail than some previous appeals to 'the natural facts', it doesn't really explain in any detail how bonding works or why it should work in this way. Recall that Schneider felt that the appeal to the natural facts of biology that the concept of 'kinship' was based on was inadequate and he doubted that such concepts could be claimed to be "models formed after the scientific facts of biology" (see above). Any discussion of the purported relationship between social bonding and 'blood' would have to provide much more detail than Goodenough does, and in doing so, may or may not support his position.

1.6 CONTINUING AMBITIONS OF SOCIOBIOLOGY'S HEIRS

Other approaches exist which claim to represent the scientific facts of biology, and claim to provide an alternative framework that can (reductively) encompass all of the social sciences. *Evolutionary psychologists* have the goal of replacing existing social science perspectives which, it is claimed, rely on what is labelled a 'Standard Social Science Model' (SSSM) (Tooby & Cosmides 1992). Evolutionary psychologists criticise in particular claims of the flexibility of human culture, as Pinker demonstrates in his summary of the alleged 'three key fallacies' of the 'SSSM';

> "The first is John Locke's doctrine of the tabula rasa, the Blank Slate: that the human mind is infinitely plastic, with all its structure coming from reinforcement and socialization." (Pinker 1999, 191)

Pinker uses the below extract from Mead (1935) which, he aims to show, demonstrates commitment to a fallacious 'blank slate' concept;

> "We are forced to conclude that human nature is almost unbelievably malleable, responding accurately and contrastingly to contrasting cultural conditions… The members of either or both sexes may, with more or less success in the case of different individuals, be educated to approximate [any temperament]." (Mead, 1935, in Pinker 1999, 191)

Pinker goes on to say that;

> "The doctrine of the Blank Slate, which justifies the dismissal of people's stated wants as an artifact of a particular time and place and thereby licenses the top-down redesign of society, is a totalitarian's dream." (Pinker 1999, 201)

The other two alleged 'fallacies' of the SSSM are also given;

> "The second belief is Jean-Jacques Rousseau's doctrine of the Noble Savage: that evil comes not from human nature but from our social institutions… We see the doctrine as well in the popular image of native peoples living in peaceful coexistence with the ecosystem and with one another. " (Pinker 1999, 191-192)
>
> "The third doctrine is what Gilbert Ryle called the Ghost in the Machine: the belief that we are separate from biology, free to choose our actions and define meaning, value, and purpose." (Pinker 1999, 192)

Pinker, whose familiarity with the range of human cultures described in ethnographic material is never demonstrated, thus succinctly sums up his understanding of social science perspectives. But what new insights into understanding the diversity of human cultures can evolutionary psychologists actually contribute? Pinker gives the following account;

> "The emerging picture is that our genetic program grows a brain endowed with emotions and with learning abilities that were favored by natural selection. The arts, humanities, and social sciences, then, can be seen as the study of the products of certain faculties of the human brain. These faculties include language, perceptual analyzers and their esthetic reactions, reasoning, a moral sense, love, loyalty, rivalry, status, feelings toward allies and kin, an obsession with themes of life and death, and many others. As human beings share their discoveries and accumulate them over time, and as they institute conventions and rules to coordinate their often conflicting desires, the phenomena we call "culture" arise." (Pinker 1999, 188)

The majority of evolutionary psychologists have generally avoided revisiting anthropological data on social bonds. However there are some who subscribe to Tooby and Cosmides' critique of the social sciences (Daly & Wilson 1996, 23), and have worked on kinship and social bonding. Daly and Wilson have particularly looked at step-parental families (in North American and British society), and have attempted to apply biological theory to their data. However, the interpretation of biological theory is no different from the incorrect interpretations of other sociobiologists, in this case, Alexander (1979) (see chapters 2 and 3 for a review);

> "Hamilton replaced the classical Darwinian conception of organisms as evolved *reproductive strategists* with the notion that they have evolved to be *nepotistic strategists* (Alexander, 1979). One implication of this theory is that any socially complex species is likely to possess psychological adaptations tending to soften potentially costly conflicts among genetic relatives… The general rule is that the intensity of conflict is adjusted nepotistically in relation to available cues of kinship. There is no obvious reason why human beings should be an exception." (Daly and Wilson 1999, 63, emphasis in original)

> "Evolutionary thinking led to the discovery of the most important risk factor for child homicide - the presence of a *stepparent* (Daly & Wilson, 1996). Parental efforts and investments are valuable resources, and selection favors those parental psyches that allocate effort effectively to promote fitness. The adaptive problems that challenge parental decision making include both the accurate identification of one's offspring and the allocation of one's resources among them with sensitivity to their needs and abilities to convert parental investment into fitness increments… Stepchildren were seldom or never so valuable to one's expected fitness as one's own offspring would be, and those parental psyches that were easily parasitized by just any appealing youngster must always have incurred a selective disadvantage." (Daly & Wilson 1999, 64-65, emphasis in original)

However, similar research undertaken in a different society (Sweden) finds very distinct social patterns. Such findings contrast sharply with evolutionary psychologists' claims to be giving an objective ('biologically accurate') view of 'human nature'. The researchers involved suggest that Daly and Wilson do not pay enough attention to cultural factors;

> "In summary, our results do not support the conclusion that step-parenthood is the most important risk factor for child homicides in families (Daly & Wilson 1998). Furthermore, the differences in risks between Canada and Sweden suggest that cultural factors influence patterns of child homicide." (Temrin et al. 2000, 945)

Subscribing to the sociobiologists' interpretation of biology theory, it is no surprise that evolutionary psychologists have, for the most part, avoided attempts to apply their hypotheses to the ethnographic evidence on 'kinship' (but see Daly et al. 1997, discussed in chapter 3.5 below). Unfortunately, some established cultural anthropologists themselves have returned to elements of the earlier sociobiological ideas on 'kinship' (Bloch & Sperber 2002). Bloch and Sperber's account carefully eschews the interpretation of biological influence as a kind of teleological force, which characterised some early sociobiological approaches. However, like sociobiologists, they too follow a simplistic interpretation of the basic biological theory (which requires careful interpretation lacking in all these analysis, see chapters 2 to 6);

> "The potential contribution of kin altruism to what is known as "inclusive fitness" favors the emergence of a disposition to helpful behaviour adjusted to genealogical distance between the altruist and the beneficiary. For such a disposition to exert itself, the organism must have the possibility of discriminating kin from nonkin and, among kin, degrees of relatedness… Let us accept, as a hypothesis, that there is an evolved disposition to try to differentiate people in a way sensitive to their degree of genealogical relatedness to self. It is most unlikely that such a disposition would be such as to cause the individual to seek actual genealogical information. It would rather be a disposition merely to seek whatever available information might indicate relatedness to self. Now, such a disposition would favor the cultural stabilization of systems of representation providing for such ego-centered differentiation without determining their exact nature." (Bloch & Sperber 2002, 730-731)

As is clear in the extracts, all these interpretations *claim that biological theory predicts that humans will engage in social behaviour on the basis of identifying their genetic relatives*. Later chapters outline an alternative model formed from the scientific facts of biology. It is clear that Schneider's question about what precisely is the relationship between the facts of biology and the social ties which characterise 'kinship' has yet to be answered. Simplistic interpretations (sociobiology and evolutionary psychology) of fundamental biological theory (see chapters 2-6) have not derived hypotheses that are able to account for the evidence. Unconvinced by such approaches, many kinship theorists (see Schweitzer, above) nevertheless feel that kinship must have *something* to do with procreative ties. The current thesis attempts to contribute to these debates, and to show where and how cultural and biological perspectives may be compatible.

1.7 A BROADER CONCEPTION OF 'BIOLOGY'

Recent ethnographic accounts of social bonding emphasise cultural conceptions, and don't privilege procreative links or 'blood ties'. Nevertheless, Carsten (1995) suggests that social connections may be constituted by a variety of processes in which 'biological' and 'social' processes may be indistinguishable;

> "Ideas about relatedness in Langkawi show how culturally specific is the separation of the "social" from the "biological" and the latter to sexual reproduction. In Langkawi relatedness is derived both from acts of procreation and from living and eating together. It makes little sense in indigenous terms to label some of these activities as social and others as biological." (Carsten 1995, 236)

More recently, Carsten has edited a volume *Cultures of Relatedness* (2000), a central theme of which she suggests;

> "[I]s the relationship between the 'biological' and the 'social'. If 'biology' or 'nature' has been the grounding for the 'social' in the West, and this relationship now appears to have been 'destabilised', can we put our understanding of this process of destabilisation to work in studies of non-Western cultures? What kind of relevance does this breaching of our foundational certainties have for how we understand and compare relatedness cross-culturally? …The chapters which follow suggest not only that biology does not everywhere have the kind of foundational function it has in the West, but that the boundaries between the biological and the social which, as Schneider demonstrated, have been so crucial in the study of kinship are in many cases distinctly blurred, if they are visible at all. These new understandings may force us to conclude that kinship needs to be reinvented in a post-modern, or – to use Bruno Latour's (1993) term – 'non-modern' spirit." (Carsten 2000, 3)

As will be illustrated in later chapters (chapters 7 and 8), ethnographers working in some cultures are finding that the processes that create social bonds are conceived to derive not from genealogical connections (Schneider's 'being'), but from nurturing, sharing and other processes of 'doing'. What, if any, is the connection between such *processes* and 'the biological'?

In his work on *Separation and Reunion in modern China,* Stafford (2000) discusses psychologists' work on the processes of forming social attachments and responses to separation, in both humans and other primates. The existence of such social instincts across species, Stafford suggests, may have implications for cross-cultural research on 'relatedness' (amongst other things);

> "...Bowlby argued that *attachment behaviour in humans and other animals is instinctive,* i.e. that evolutionary pressures have selected this psychological trait... Now: might Bowlby's realist approach – which defines these behaviours as universal and instinctive, which examines their consequences through naturalistic observation, and which stresses their central role in intensifying human relatedness – be a useful starting point for anthropologists?… Extrapolating from the work of Myers [on emotions], one could make the case that *all* anthropological discussions of relatedness – e.g. the accounts by Malinowski, Mauss, and a great many others of the ways in which gift exchange and reciprocity, or commensality and the sharing of 'substance', help to constitute human relatedness – are also by definition, dealing with intractable problems of attachment and separation in social life." (Stafford 2000, 12, 24, emphasis in original)

Here then is a focus on the universality of the psychological potential that gives rise to attachment, and the suggestion that attachment mechanisms and associated emotions are involved with 'relatedness' and social life. Stafford, following Bowlby, traces these instincts to other primates. Could it be that through this kind of investigation of basic 'biological facts' (those observable in humans in common with other species) useful insights might potentially emerge? A similar point is made by Carrithers at the conclusion of a brief review of debates over nature and culture in social science;

> "Humans do vary greatly in their cultural endowments and those endowments bear heavily on their behaviour; yet humans, like other animals, came into being through forces best described as Darwinian. It follows then that humans evolved to have culture, so to speak: our big brains with their ability to manipulate symbols, along with our abilities to use our own respiratory tracts for speech, comprise the Darwinian heritage that makes us the culture-bearing animal *par excellence.* This much

> might be admitted by even a very reductionist biologist or a very doctrinaire cultural anthropologist. What is only now coming to light, however, is a subtler picture, which shows that we have evolved not in the first instance as culture-bearing animals, but as social animals. Studies of childhood cognitive and emotional development, and comparative studies of other primates, show that beneath and around the stuff of culture, there stands a scaffolding of social abilities and a distinctly social intelligence. We can learn culture because we come richly equipped, even as the smallest infant, to enter into conscious and responsive social relations with our fellows. We become culturally knowledgeable because we first become socially knowledgeable, able to grasp and react to the moods and intentions of those around us in a way recognisably akin to, but a good deal more powerful than, that of our primate cousins." (Carrithers 1996, 395-6)

What these various observations suggest is that, for at least some ethnographers actively involved in documenting culturally specific concepts and practices, certain kinds of social instincts nevertheless appear to operate. Can an account be found which demonstrates that biology, psychology and the ethnographic findings on social ties are essentially compatible?

Once the 'biology' is delineated, this facilitates a clearer focus on the varieties of kinship (i.e. patterns of social interaction) as practiced in different cultures and the variety of processes which lead to that variability. If the biological factors can be clearly defined, understood and held constant in an analysis, the role of the various historical, economic, ecological, demographic and cultural factors, mentioned by Schneider (section 1.2, above) in shaping and forming practices of social bonding in different societies, can potentially be seen more clearly.

1.8 SUMMARY

It is important to notice that the claim of the current research is *not* that an understanding biological factors can explain everything that is interesting about social patterns in human societies. The approach is not reductive. The claim is rather that a thorough investigation of the 'biological facts' can be useful mainly though allowing a change in focus as to how social bonding instincts operate; away from confusion about the place of genealogy in social ties, and onto a reformulated baseline, built around varied processual aspects of social bonding. On the one hand, ethnographic study is in a unique position to document the variety of forms that these underlying processes and their cultural conceptions take, and the variety of 'kinship' patterns they give rise to, as work such as that of Carsten's and of many other ethnographers (reviewed in chapter 8 & 9) has already illustrated. On the other hand, this potential clarification of the long-standing confusion over biology may allow us to move further towards the pressing task of investigating the salience of variables such as political economy, ecology, demography, and others, in shaping social bonding and kinship patterns.

CHAPTER TWO – EVOLUTIONARY BIOLOGY THEORY

2.01 INTRODUCTION

The last chapter suggested that the conflation between conceptions of 'social ties' and 'blood relationship' which characterised anthropological approaches to the study of kinship (Schneider 1984), has had a parallel in treatments of social relationships claiming to be based on 'biological facts', especially sociobiological approaches emerging in the 1970s. This chapter will review the biological theory that sociobiological approaches claim to represent, and some discussions relevant to interpretation of the theory. I will suggest that the biological theory cannot be interpreted to necessarily predict that individual organisms *will cooperate* with genetic relatives. The following chapter will review the classic sociobiological interpretations of the theory, and highlight their errors.

The basic theoretical position in biology, *'inclusive fitness'* theory (Hamilton 1964, 1970, 1972, 1975), is by now widely employed for modelling the evolution of social behaviours. I will argue (as others have, e.g. Dawkins 1982) that the basic model is powerful as a treatment of *the selection pressures* on the *evolution* of genes and behavioural dispositions, but needs careful interpretation. I will suggest that some errors of sociobiological applications have stemmed from an over ambitious attempt to extend inclusive fitness theory beyond its domain as an evolutionary level explanation (an 'ultimate explanation') into a predictive theory applied directly to *the expected outcomes* of animal behaviour (a 'proximate explanation'), and particularly to that of humans. This ambition was partly fuelled by a misunderstanding of the scope of the basic theory.

The chapter begins by describing how biological theory creates a working definition of 'social behaviour' (section 2.02). Then an introductory overview (section 2.03) of the current critique of common interpretations of the basic theory is given (readers unfamiliar with the basic theory may wish to refer back to this later). The main content of the chapter is then broken down into two halves; Part 2.1 describes basic inclusive fitness theory, as I interpret it. Part 2.2 reviews various treatments of the theory, including Hamilton's original papers, with the aim of demonstrating that the interpretation set out in part 2.1 is fair and justified. The chapter ends

(2.2.5) by briefly looking at some more 'in depth' issues of interpretation (dealt with more fully by chapters 4 to 7). The aim is to equip the reader with enough knowledge to understand the critique of early sociobiological approaches to human kinship, conducted in the next chapter.

It may be worth noting that, just as with Darwin's original work on natural selection, (see chapter 1) which sought to explain how biological evolution occurs, Hamilton's model was an attempt at illuminating a biological phenomenon which needed a theoretical treatment; the evolution of social behaviour patterns. It was intended to describe a process, rather than to make claims about the desirability or moral value of that process (such as 'Social Darwinism' interpreted Darwin's Natural Selection).

As mentioned in chapter one, an additional part of the confusion in the application of inclusive fitness theory to humans is due to terminology. The theory has often been identified with 'kin selection', which has confusing connotations for anthropological application. Although I avoid the term 'kin selection' here, preferring to discuss basic inclusive fitness theory (Hamilton 1975, Dawkins 1982), the term does occur in some of the references cited.

2.02 SOCIAL BEHAVIOUR IN THE EVOLUTIONARY BIOLOGY FRAMEWORK

The 'Modern Synthesis' (of Darwinian evolutionary biology and Mendelian genetics), with its roots in the 1920s and 1930s, is the established theoretical framework within which to understand biological evolution. According to this perspective, the evolutionary process is driven mainly by *environmental change*, *random mutation* (and *recombination*), *genetic drift*, and a mechanism of *natural selection* acting, via *differential reproductive success* (or 'fitness'), on gene (or allele) frequencies. Natural selection acts on the differential reproductive success of heritable factors (genetic material, genes); genes whose presence positively covaries with reproductive success tend to be preserved by natural selection (Price 1970, more below). As well as acting on genes which influence organisms' physical characteristics, genes influencing behaviours are also understood to be subject to these same selective pressures.

The contribution to reproductive success of both physical and behavioural characteristics cannot operate (or be considered) in abstraction from their *environmental context*. No characteristic can be said to evolve *per se* in abstraction from the environment it typically exists within. To the extent that environments change, established characteristics previously 'selected for' (i.e. increasing in frequency) can subsequently be 'selected against' (decrease in frequency). Variations in heritable characteristics are initially produced by random genetic mutations and recombination (e.g. via sexual reproduction). Genes and characteristics become established in a population partly as a result of drift effects, and of the statistical reproductive consequences ('covariance with reproductive success') of their effects in their typical environment, and obviously cannot be said to *pursue* these effects as goals (the pathetic fallacy). Biological analyses are nevertheless often accompanied by notions of 'progress', and a seeming assumption that certain characteristics are somehow a goal of the biological process. (See also Huxley 1893, chapter 1.3.1).

The relevance of *social* interactions and social behaviours to natural selection comes when such behaviours may have consequences for the ultimate reproductive outcomes of the organisms (and thus the genes) involved, both those genes in the social 'actor' and genes in the recipient(s) of the effects of the behaviour. Thus, in order to analyse the *evolution by natural selection* of any underlying genetic basis to species-typical forms of 'social behaviour' we can adopt a formal view of the behaviour in terms of its typical affect on reproductive success. A broad definition of social behaviour thus becomes *interactions which have consequences for the reproductive success of the individuals involved*. The utility of such a broad definition is that it allows the consideration of the evolution of any characteristic which is expressed in an interaction between individuals.

Within biology, the established approach to understanding the evolution of such social behaviour, via natural selection acting on the frequencies of genes that influence it, is encapsulated by *inclusive fitness* theory (where *fitness* refers to reproductive success), first formulated by Hamilton in the early 1960s (Hamilton 1963, 1964) and elaborated and refined through subsequent work (e.g. Price 1970, Hamilton 1970, 1972, 1975, Grafen 1985, Queller 1992, Frank 1997). Hamilton, trained in the quantitative genetic techniques of the 'Modern Synthesis', produced a way of analysing how the mechanism of natural selection acts on the frequency of genes and characteristics that have effects that can be considered 'social' in the sense of the above definition (1964). The available tools of quantitative genetics were not well suited to what was necessarily an analysis of the *interactions* between plural individuals, and the plural genetic consequences summed over such individuals (the *inclusive* consequences), and the formal core of Hamilton's early (1964) model contained some inaccuracies (Hamilton 1996). Subsequent refining of the basic formulation of the mechanism of natural selection by Price (1970) allowed Hamilton to formulate a more straightforward and accurate analysis (1970, 1972, 1975, see below).

Inclusive fitness theory, through various refinements, is now well established and serves as a guide to analysis of the evolution of social behaviours of a huge variety of organisms. This quantitative approach to analysing the evolution of unreciprocated ('altruistic') social behaviours was supplemented in the early 1970s by work on reciprocal (exchange) social behaviour by Robert Trivers (Trivers 1971, 1972, 1974). Potential interplay between these two proposed selective forces may provide additional insights into the evolution of traits in group living species but is only touched on in the current thesis. Despite being the dominant paradigm in biology, no derivation of inclusive fitness theory has yet been found that accommodates the full range of human kinship patterns (Hamilton 1996). The current work proposes a way to solve this problem by arguing that the apparent clash with ethnographic (human) evidence results from common misinterpretations of the theory (exemplified by early human sociobiological approaches, reviewed in chapter 3). An alternative approach is provided which, it is argued, can accommodate the full range of human kinship patterns.

2.03 SUMMARY OF THE PRESENT CRITIQUE

In this and the following chapter I demonstrate that, despite many cautionary and clarifying discussions from leading theorists about how inclusive fitness theory should be interpreted (section 2.2.5 below), too often the implications of the basic theory are not correctly understood. The full details of the critique will emerge later in this chapter and subsequently. However, to serve as a guide, I here set out some logical foundations relevant to evolutionary biology as a whole, including inclusive fitness theory, and outline what I believe should be focused on. Many of these points are repeated in an expanded form in the following sections. The critique of sociobiological applications to human behaviour will be illustrated by examples in the next chapter.

As mentioned above, inclusive fitness theory is too often interpreted to mean that social behaviour between relatives *per se* is a goal of evolution. This kind of teleological error, based on incautious extension of metaphors, is common in evolutionary biology, and particularly pertinent here. As a corollary (and key within the current thesis, see Chapter 1), inclusive fitness theory is often interpreted to imply that genes (or even individual organisms) are selected to evolve ways of actively distinguishing the identity of close genetic relatives *in order to* preferentially engage in social behaviours with such individuals. The rationale for this is that *by doing so they would benefit* the "inclusive fitness of the individuals (and genes) involved".

Over employing adaptationism, functionalism, and invoking strategies and 'goals', all risk undermining key tenets of evolutionary theory, which explicitly rejects teleology, instead proposing a random, consequential and undirected biological process. Notions of 'individual inclusive fitness' can only be metaphorical extensions of the basic description of selection pressure, and must be carefully employed; they have been central to the misinterpretation (see also Dawkins 1976, 1982). In particular, there needs to be a careful distinction made between the notion of an evolutionary *'selection pressure upon'* genes relevant to social interactions to correlate with certain kinds of net reproductive outcomes (e.g. statistically meeting the inclusive fitness criterion); and the simple sounding but *incorrect* notion that genes or individuals are *'selected to achieve a goal of'* behaving socially towards relatives, reflected in the form in which behaviours are *expressed*. The latter notion makes the error of taking too literally the metaphorical short-hand way of understanding natural selection; confusing a description of (ultimate) *evolutionary* selection pressure for a description of the (proximate) *expression* of behaviour. Inclusive fitness theory simply specifies a necessary condition, or 'criterion' upon the evolution of certain kinds of social behaviour within a species. What particular forms of social behaviour might evolve, and by what proximate mechanisms these might be expressed, are not specified by the theory. However, very often the theory is interpreted as specifying a rule governing the expression of social behaviour, in particular, that organisms 'have evolved to' direct such behaviour towards genetic relatives. This is incorrect.

The notion that social behaviour itself is a goal of the evolutionary process, and the further notion (mistakenly attributed to inclusive fitness theory) that individuals are expected to attempt to identify their genetic relatives and engage in social behaviours with them, also both disregard any consideration of the *environmental context* within which the evolutionary process occurs. Evolution by natural selection focuses explicit attention on the selective environment, yet consideration of environmental context is too often foregone in the operationalisation of inclusive fitness theory.

Being a theory about an evolutionary process and statistically typical outcomes in evolutionarily typical environments, investigating how inclusive fitness theory applies to a given species must begin with an analysis of the evolutionarily typical ecological niche and demographics of that species. The ecological niche occupied by the species in question may or may not provide any significant context of interaction between individuals, particularly interactions beyond one-off mating encounters (sexual species). If the basic 'life history' and niche of the species under study does not lead to significant encounters between the individual organisms, then selection pressure upon characteristics which are 'social' (according to the above definition, section 2.02) will be weak or non-existent. For species occupying such niches, species-typical 'social behaviour' characteristics are thus not expected to have evolved (see also Sherman 1980, below). Consideration of the statistical probability and potential patterns of interaction of individuals in typical past ('evolutionarily significant') environments must come into an investigation of '*evolved* social behavioural tendencies'; i.e. those posited to now be species-typical, and which are under investigation as such.

A context of interaction is thus a prior *necessary condition*. It must be present before 'social behaviours' which are expressed in that context are potentially brought into being by mutation and acted upon by selection. Inclusive fitness theory's domain of relevance is thus limited to outlining details of the selection pressure that applies *when such a context does exist*. The insights of this theory become relevant if such 'potential' exists, and the theory's particular insight is to point to consideration of the statistical associations of replica genes in such a context (more below). This non-teleological interpretation of Hamilton's theory, placing emphasis on ecological context and 'potential', is sometimes discussed. As Silk (2001) put it;

> "The role of kinship [genetic relatedness] in the daily lives of animals depends on the demographic composition of the groups in which they live. Kin selection [inclusive fitness] will only be an important force in the evolution of social behaviour if animals find themselves in situations where they have an opportunity to fulfil the predictions of Hamilton's rule. At a minimum, kin must be available. The number, availability, and degree of relatedness among kin will depend on how groups are constructed in nature." (Silk 2001, 77)

Consideration of the typical interaction context occurring in past (evolutionarily significant) environments needs to be guided by a consideration of the relevant demographics of the species (Sherman 1980, 1981, Tang-Martinez 2001, see later quotes in section 2.1.6). Does the ecological niche provide opportunities for the clustering of individuals in groups or are individuals typically solitary? Much 'socioecology' research (reviewed in chapters 4 and 5) has suggested that a fundamental influence on demographic patterns is the type and distribution of primary food sources and patterns of predation. To consider potential patterns of statistical association of replica genes; typical patterns of dispersal, mating system, litter size (and other demographic variables) need to be taken into account. The importance of investigating these variables will be further discussed and illustrated in chapters four and five.

2.1 PART ONE: HAMILTON'S INCLUSIVE FITNESS THEORY

2.1.1 CONTEMPORARY THEORIES PRIOR TO HAMILTON

At the time of Hamilton's innovation, the predominant existing framework within biology for explaining social behaviour was that it could evolve by selection due to its 'benefit to the group'. Hamilton (1996) gives the following example from Wigglesworth's (1964) *The Life of Insects;*

> "Insects do not live for themselves alone. Their lives are devoted to the survival of the species whose representatives they are… We must now stand back and look at the insect as a member of the 'population' or 'species' to which it belongs. Indeed we have reached the heart of the matter – the aim and purpose (so far as we can understand them) of the life of insects." (Wigglesworth 1964, cited in Hamilton 1996, 22)

This 'species-advantage' reasoning had been popular since before the mechanisms of heredity were understood through Mendel's work. However, since the 'Modern Synthesis' (or as Hamilton below refers to it, 'Neodarwinism') had placed *changing frequency of genes* via their affect on individual reproduction as the central metric of evolution, strictly, social behaviours should be amenable to analysis in this light or an alternative formal framework advanced. However, many biologists continued to refer vaguely to group-level benefits as the explanation for the evolution of individual social behaviour, despite the rejection of this mode of reasoning by leading theorists (Fisher 1958, Wright 1948, cited in Hamilton 1996 [1963]). The group-selection perspectives were not formalised with models demonstrating the selection pressures on gene frequency change. Hamilton summarised this dualism in a later review;

> "Until the advent of Mendelism uncritical acceptance of group selection could be understood partly on grounds of vagueness about the hereditary process. For example, courage and self-sacrifice could spread by cultural contagion and, in so spreading, modify heredity as well [if inheritance were 'Lamarckian']. But in the event neither the rediscovery of Mendel's work, nor the fairly brisk incorporation of Mendelism into evolutionary theory had much effect. From about 1920 to about 1960 a curious situation developed where the models of 'Neodarwinism' were all concerned with selection at levels no higher than that of competing individuals, whereas the biological literature as a whole increasingly proclaimed faith in Neodarwinism, and at the same time stated almost all its interpretations of adaptation in terms of 'benefit to the species'. The leading theorists did point out the weakness of this position, but on the whole concerned themselves with it surprisingly little." (Hamilton 1996 [1975], 331)

There are great difficulties with these informal assumptions that all forms of social behaviour evolve solely via their impact on the group's reproductive advantage ('naïve group selection'), which will emerge below. A simultaneous problem was that the classical theory of the modern synthesis only allowed for the spread of genes via an individual's own direct reproduction to be considered and calculated in a gene's frequency change. Because of this perspective, the classical theory had no established method of accounting for (i.e. quantifying and analysing) the effects of individuals' *interactions* on each other's reproduction. This meant that the classical theory effectively could not analyse the selective pressure on 'social behaviour' as we have defined it. Hamilton identified this gap, and suggested that it was partly due to this discrepancy that informal group selection arguments were often employed to fill the void. ('Social behaviour' was in a sense treated as a property of the group, not as an individual behavioural characteristic). Here is his analysis of the situation from his 1963 paper;

> "It is generally accepted that the behaviour characteristic of a species is as much the product of evolution as the morphology. Yet the kinds of behaviour which can be adequately explained by the classical theory of Natural Selection are limited. In particular this theory cannot account for any case where an animal behaves in such a way as to promote the advantages of other members of the species not its direct descendants at the expense of its own. The explanation usually given for such cases and for all others where selfish behaviour seems moderated by concerns for the interests of a group is that they are evolved by Natural Selection favouring the most stable and co-operative groups. But in view of the inevitable slowness of any evolution based on group selection compared to the simultaneous trends that can occur by selection of the classical kind, based on individual advantage, this explanation must be treated with reserve so long as it remains unsupported by mathematical models." (Hamilton 1996 [1963], 6)

'Individual advantage' here simply means the conventional notion of an individual's direct reproductive success. The classical theory suggested that genes will gain in frequency (spread) depending upon their affect upon individual direct reproductive success. The possibility of natural selection acting on gene frequencies via 'group selection' requires *differential survival and reproduction of groups associated with variance in gene frequencies* (Price 1970, Hamilton 1975). If the high frequency of certain genes within a group tends to result in high reproductive success of that group (relative to differently constituted groups), as a consequence, those genes will tend to increase in frequency within the sum of groups (i.e. the species). Such genes and the traits associated with them will thus gradually become species typical. Observing this possibility, albeit informally specified, the 'group selection theory' of social behaviour proposed differential reproduction between groups to be the major cause of the evolution of social behaviours.

What precisely is meant by a 'group' is itself in need of some analysis, and comparatively few species live in 'groups' as the term is generally understood (this will be considered further below). Those groups which contain individuals bearing such genes are assumed to out-reproduce those that don't, and this is proposed to be a more important influence on what genes/behaviours become species typical than selection acting on genes via differential individual reproductive success *within* the group. A necessary component of the view that such genes could spread via group-selection is that any marginal cost to its own reproductive success that a bearer of such gene might suffer relative to other individuals in the group, is outweighed by the extra-reproduction that comes to such individuals from being members of such a group. This would be the case if the group containing the 'altruists' survives whilst groups without altruists die-out, or shrink; such that (despite the trend 'within the group') the group itself is effectively out-reproducing the other groups. The balance of selective forces (treated quantitatively only later by Price 1970) is assumed to have the net result that the individual behaviour evolves to put the interests of 'reproduction of the group' above those of the individual.

In the above quote, Hamilton noted that the group-selection reasoning is usually invoked without careful quantitative argument or formal models. Hamilton's 'inclusive fitness' models (1964, 1970, 1972, 1975) provide the analytical and conceptual tools for deconstructing what we mean by the evolution of 'social behaviour'. As we have defined it here (section 2.02 above), social behaviour could take on a range of forms, but the more general 'altruism to any member of your group' is undefined in terms of the size/constitution of the group as well as what degree of altruism we have in mind (see 'Hamilton's rule', section 2.1.5 below). Thus one of the advantages of inclusive fitness theory is that it forces analysts to think carefully and quantitatively about what kind of ‘social behaviour’ is under study (or being treated as ‘species typical’) in terms of what is the genetic association of the ‘group’ (or individual) it typically benefits and what ‘degree’ of altruism is involved.

I discuss the details of Hamilton’s model further below. In order to introduce it, I first review his analysis of the quantitative problems that accompany the group selection model, since these are the problems his own model was designed to clarify. Some of the key variables that he considered to be involved in the evolution of social behaviours are apparent in Hamilton’s (1963) review of a (rare) treatment of the possibility of generalised altruism evolving by group selection, that had been given by Haldane (1932);

> “Haldane supposed an increment to group fitness (and therefore the rate of group increase) proportional to its content of altruistic members and showed that there could be an initial numerical increase of a gene for altruism provided the starting gene frequency was high enough and the individual disadvantage low enough compared to the group advantage conferred. He concluded that genetic altruism could show some advance in populations split into ‘tribes’ small enough for a single mutant to approximate the critical frequency. He did not, however, sufficiently emphasise that ultimately the gene number must begin to do what the gene frequency tends to do, *ex hypothesi*, from the very first; namely to decrease to zero. The only escape from this conclusion (as Haldane hints) would be some kind of periodic re-assortment of the tribes such that by chance or otherwise the altruists became re-concentrated in some of them.” (Hamilton 1996 [1963], 6-7)

As noted above, within the classical theory, the analytical tools for weighing selective effects at the intra-group level (individual disadvantage) versus effects from inter-group differential reproduction (group advantage) did not exist. Yet, Hamilton here demonstrates that a consideration of the reproductive trend at both levels is necessary to understand the trend at the meta-population level and thus which genes/behaviours are likely to become species typical. This essence of what variables need evaluating was fully clarified by Price (1970) who was influenced by Hamilton’s papers (Hamilton 1996).

To summarise Hamilton's deconstruction; assuming a high starting frequency, the local *frequency* of a gene 'for generalised altruism' within a social group comprised of a number of individuals of differing genotypes (for the gene locus under consideration) will always be declining (based on our definition of the reproductive effects of the gene), to the benefit of alternative alleles. However, its actual *number* may nevertheless be increasing. Only within more highly concentrated sub-groups could a gene encouraging *generalised* altruism maintain such an increase in actual-numbers and 'individual disadvantage' be outweighed by 'group advantage'. But when the gene eventually drops below the critical frequency within a group, the actual numbers of the gene will also decrease. Thus the need for regular group restructuring (of a non-random kind) referred to by Hamilton, to maintain the critical frequency. Additionally, for this process to maintain the gene at significant frequencies at the meta-population level, we must posit that the process of non-random re-concentration is going on across all sub-populations.

Essentially Haldane's argument becomes; if only the initial conditions could be arranged, and the necessary regular biased re-association occur, such a gene could spread. Clearly this suggestion begs the question of how such initial conditions could realistically occur, and further; what do we mean by generalised altruism if we are simultaneously posit that it regularly re-associates itself with 'its own kind'?

This brings us back to the relevance of Price's insights and Hamilton's quantitative models. The necessity for 'concentration' of a gene in a group is obviously key. Price and Hamilton approach this via consideration of the frequency of a gene in a group, or more accurately the variance in frequency of a gene in a group relative to the effects the presence that gene has on the reproductive success of that group (Price 1970). This is calculable for any size of group (or population) and even for any number of sub-populations within a larger population (which might be the entire species, Hamilton 1975). More on this below.

This consideration of gene's frequency within the group of interest further suggests the importance of clear thinking about what one means by a 'group'. Depending on how we define our group, a gene may be at higher or lower 'concentrations' (in the sense of frequency of the gene in the group). Are there any regularly occurring 'groupings' which have the necessary characteristic of an elevated frequency of the gene? This in turn forces us to consider what kinds of social behaviour we are interested in. Are we talking about the 'social behaviours' genes express in cells in the context of a multicellular (perhaps clonally related) body? More likely we are thinking of types of social behaviours expressed by individual organisms in the context of interactions with other individuals (this is the focus of the application of inclusive fitness theory to human social behaviours). We may for example be thinking of social behaviours expressed in infant mammals in the context of communal feeding within a 'group' of litter-mates. The discussion above suggested the importance of considering the typical patterns of interaction, regularly occurring 'grouping contexts' and thus the 'potential' for the evolution of 'social behaviours' in a species. In short, Hamilton highlighted the importance of defining the 'group' of interest (that which the behaviour is expressed within) carefully. In particular; what is the evolutionarily typical relative frequency of the relevant gene / behaviour in the group within which the behaviour is expressed?

2.1.2 HAMILTON'S INCLUSIVE FITNESS THEORY

Although Hamilton had shown that the framework that understood all social behaviour as evolving due to 'group selection' had weaknesses, he nevertheless had to advance some framework within which to understand the evolution of the varieties of social behaviour which clearly exist in nature. Hamilton's next *published* paper (1964) was actually *written* before the 1963 paper (Hamilton 1996), and its focus is narrower than both the latter and his subsequent papers on inclusive fitness theory. However, since it included a discussion of the possible applications to empirical study, it has tended to be the treatment most often cited. It essentially employs the mode of analysis suggested by Hamilton above, especially in respect to the actual frequency change of the gene that influences the 'social' behaviour, and the need for consideration of the probability that the recipients of the behaviour are typically genetically 'its own kind'. In this early paper, Hamilton illustrated his point about 'gene concentration' by focusing more narrowly on the evolution of social behaviours between close genetic relatives (what biologists call 'relatives by recent common descent'). This focus on close genetic relatives, although an approximately accurate rule of thumb for inclusive fitness theory in practical terms, actually obscures the wider theoretical point – that it is the statistical association of replica genes, however occurring, which is key (e.g. Hamilton 1975, Grafen 1990, Frank 1995). Later papers would build a more general (and strictly correct) model (as we will see below);

> "Sacrifices involved in parental care are a possibility implicit in any model in which the definition of fitness is based, as it should be, on the number of adult offspring. In certain circumstances an individual may leave more adult offspring by expending care and materials on its own offspring already born than reserving them for its own survival and further fecundity. A gene causing its possessor to give parental care will then leave more replica copies in the next generation than an allele having the opposite tendency. The selective advantage may be seen to lie through benefits conferred indifferently on a set of relatives each of which has a half chance of carrying the gene in question." (Hamilton 1996 [1964], 31-32)

Hamilton's initial novel suggestion is to view the selective advantage (given the species' possibility of 'care'), even in the familiar parent-offspring case, as coming from the gene (and behaviour) whose expression results in a benefit to individuals with a greater than average probability of carrying the gene. This genetic relatedness between parent and offspring would provide an instance of 'association with its own kind' that Hamilton (above) had shown to be necessary (section 2.1.1). This is a novel point since complex social behaviour between parent and offspring (although in fact quite rare outside mammals and birds) is assumed to be 'natural', without consideration of the conditions under which it might potentially evolve (e.g. a context of interaction), and an analysis of the relevant selection pressure. Hamilton continues;

> "From this point of view it is also seen, however, that there is nothing special about the parent-offspring relationship except its close degree and a certain fundamental asymmetry. The full-sib relationship is just as close. If an individual carries a certain gene the expectation that a random sib will carry a replica of it is again one-half. Similarly, the half-sib relationship is equivalent to that of a grandparent and grandchild with the expectation

> of replica genes, or genes 'identical by descent' as they are usually called, standing at one quarter, and so on." (Hamilton 1996 [1964], 32)

Hamilton notes that a distribution of replica genes potentially covers a wider circle of individuals than just the parent and offspring. Looking at things in this way, it is easy to see that the expression of a gene in the grouping context of an interaction between such relatives may impact upon replicas of the gene promoting the behaviour. Hamilton suggests that, rather than natural selection acting on genes only for their affect on an individual's direct reproductive success, instead the selection pressure is on a gene's typical affect on the 'net' reproductive success across all replicas – its 'inclusive fitness'. He gives a summary of the technique he uses in his abstract;

> "Making use of Wright's coefficient of relationship as the measure of the proportion of replica genes in a relative, a quantity is found the means of which incorporate the maximising property of Darwinian fitness. This property is named 'inclusive fitness.'" (Hamilton 1996 [1964], 31)

The quantitative genetics tools available for describing the probability that individuals are genetically 'of the same kind' were somewhat limited, since, as we saw above, this form of analysis was unusual. Wright's coefficient was one measure readily to hand, but one that Hamilton's later analyses (especially after Price 1970) would eschew in favour of a more correct measure of the statistical association (Hamilton 1970, 1972) which selection pressure acts upon. One weakness of this early paper was that it described the selection pressure in such a way as to suggest that it is being 'a genetic relative' which is central to the operation of inclusive fitness, rather than just being a special case of the more general qualification. This focus on genetic relatives is one reason why Hamilton's theory came to be known as 'kin selection' (kin here meaning 'genetic relative'). In fact, as Hamilton was later to state (1975, see below) inclusive fitness theory is much broader than 'kin selection'.

Recalling Hamilton's review (1963, as above) of Haldane's treatment of the selection pressures at work on generalised altruism evolving within a stable group, we saw that a crucial barrier to positive selection was that a gene for generalised altruism in a large-scale grouping context may or may not benefit alternative alleles as well as benefitting its own likely replicas. In doing so such a gene may tend to diminish its net reproduction (summing all replicas). This will depend on the comparative frequency of the gene in that 'group context', such that, when considering the selection pressure on any particular gene/behaviour *the typical context the behaviour is expressed within* becomes critical. It is this extended form of accounting for a gene's likely affect on the reproduction of its replicas to which Hamilton now gives the name 'inclusive fitness'. He proposes to investigate the possibility for positive selection of a gene via its affect on replicas through the interaction of genetic relatives, since genetic relatives (to the extent they are reliably present) tend to comprise a 'group' with an above average frequency of such a replica gene. Hamilton discusses this by analysing how the behaviour of a bearer (denoted as 'A') of such a gene might impact on the reproduction of other individuals (and genes) within a group;

> "Every effect on reproduction which is due to A can be thought of as made up of two parts: an effect on the reproduction of genes identical by descent with genes in A, and an effect on the reproduction of unrelated genes. Since the coefficient 'r' [Wright's coefficient of relationship] measures the expected fraction of genes identical by descent in a relative, for any particular degree of relationship this breakdown may be written quantitatively…" (Hamilton 1996 [1964], 35)

Without trying to reproduce his attached mathematical models here, the mode of Hamilton's analysis is clear; the selective consequences of a gene influencing social behaviour can be analysed in terms of their impact on replica copies of the gene, relative to their impact on alternative alleles in the population. It is on the basis of this relative contribution to its own replicas' reproduction that, Hamilton suggests, a gene will be selected or not.

2.1.3 SO WHAT IS GENETIC RELATEDNESS?

The coefficient of relationship in the 1964 paper was used to quantify the probability of *'a' replica gene* being carried by the recipient of a social act. Hamilton employed Wright's 'coefficient of relationship' to provide this probability. Hamilton's later papers re-identified his quantification of genetic association with a ‘regression coefficient’ of relatedness, rather than with Wright’s narrower correlation coefficient (Hamilton 1970). Strictly speaking his use of Wright’s coefficient was inaccurate for the purpose he intended it; as a tool for analysing general selection pressures on genes via their influence on social interactions.

A regression coefficient reflects the selective pressures more correctly because it is a measure of the comparative *variance* in frequency of a gene between the host expressing the gene and the recipient(s) of the gene’s effect. Wright’s coefficient was closer to a correlation coefficient (Michod and Hamilton 1980), which, although accurately giving the probability of a two individuals sharing a gene by recent common descent, doesn’t include consideration of the ‘mean’ (average) frequency of that gene in the population of interest. This makes it suitable only for limited application with somewhat unrealistic assumptions (e.g. no homozygosity / ‘inbreeding’). The variance in frequency from the ‘mean’ (the standard deviation) is important because, in selection terms, it is not enough for the behavioural effect of the gene simply to benefit another copy of the gene. In order to *spread* (increase in frequency) and become species-typical, the behaviour should affect recipients whose own frequency of the gene is marginally higher than the existing (‘mean’) gene frequency in the population. Were a gene’s affect to fall upon an individual/group with lower than mean gene frequency, the effect can only diminish the frequency of the gene in the next generation. This was Hamilton’s (1963) essential critique of Haldane’s model. Here is an example of Hamilton’s own discussion of his use of the coefficient of relatedness;

> “The original argument was based on a supposedly infinite population in which the total average relatedness of an individual to other members of the population was zero. With realistic finite populations this is not quite the case; the criteria for ideally adaptive behaviour are then more complex and involve consideration of the general average relatedness. I report here a synthesis of unpublished work by Price and my results…” (Hamilton 1996 [1970], 178)

and again;

> "What is *R* in equation (1)? On the basis of a particular outbred model, Hamilton (1963, 1964) claimed that Wright's (1922) 'coefficient of relatedness' was the required *R*. However, later, giving a heuristic development but no further model, Hamilton (1971, 1972) modified his identification of *R* with Wright's coefficient by claiming that equation (1) requires, in principle, a regression coefficient of relatedness of genotype of recipient on genotype of altruist, whereas Wright's coefficient is the corresponding correlation coefficient. Such a correlation coefficient will often be the same but differs when the interactants are inbred to different extents." (Michod & Hamilton 1980, 694-695)

2.1.4 INCLUSIVE FITNESS THEORY'S QUANTIFICATION OF VARIOUS COEFFICIENTS OF RELATEDNESS

In this section, we look briefly at the quantitative values inclusive fitness theory typically attributes to genetic relatives. The value of 'r' represents, as discussed above, the frequency of a gene in a potential recipient of social behaviour, relative to the frequency of the gene in the actor. Its method of calculation can be found in Hamilton 1970, or Hamilton 1972 (see also Wright 1922, Haldane & Jayakar 1962 for background). Wright's coefficient, was designed as measure of the *probability* of a replica gene being present in the recipient, relative to the actor (and was fairly accurate for rare recessive lethal genes problematic in selective breeding, its original domain of application). The regression coefficient incorporates this value, but weighs it by the background (average or 'mean') frequency of the gene in the population, which gives the frequency of the gene in the recipient before the additional probability of 'identity' deriving from genealogical relationship is even considered. This consideration of the average frequency of the gene is relevant to the comparative valuation of the reproductive success of the social actor and recipient(s), since it will be reflected in the chance the gene is already carried by each, in addition to the elevated probability of 'sharing' it that we are positing the two individuals have as a consequence of their close genealogical connection (Hamilton 1970).

Taking into account the background frequency of the gene in the population of interest, the regression coefficient is therefore *not strictly* a fixed value for any particular class of genealogical relationship across all frequencies. The value of ‘r’ in diploid species, with strictly no inbreeding, approximates to values of 0.5 between parent and offspring; 0.25 between half siblings; 0.5 between full siblings; 0.25 between grandparent/ grand-offspring; 0.125 between ‘cousins’, and so on. Degree of inbreeding is influenced by such variables as typical patterns of exogamy, size of the effective breeding population, migration rates etc. For example, the actual coefficient of relatedness between what are apparently cousins then depends on the coefficient of relatedness between the two sets of parents of those cousins since, under inbreeding, this may not be zero. Inbreeding considerations thus add greater complexity to the coefficient of relatedness, and Hamilton (1972) notes;

> “[W]e do not yet know how to calculate [the relatedness coefficient] and [background gene frequency] precisely in a population that is undergoing selection, and difficulties in the interpretation of genomic inclusive fitness also remain in cases of inbreeding.” (Hamilton 1996 [1972], 273)

2.1.5 HAMILTON’S RULE

Hamilton’s analysis centred around a gene’s potential “effect on the reproduction of genes identical by descent with genes in A” (1964, 35; see the full quote above) and he noted that the coefficient of relatedness gives the expected frequency of identical genes. The other factor that requires consideration when weighing ‘inclusive fitness’ is therefore the net ‘effect’ of the behaviour itself on the reproduction of the two - the ‘cost’ to the actor’s reproductive success and the ‘benefit’ to that of the recipient(s) of the behaviour. In order to simplify the analysis it is assumed that costs and benefits to reproductive success are simply ‘additive’ (for discussion see e.g. Altmann 1979, Grafen 1984, 1985), i.e. that the ‘units’ of reproductive success by which we quantify the relative costs and benefits are equivalent.

Hamilton found a way of expressing the selection pressure on the relationship of these variables of ‘relatedness’ ‘cost’ and ‘benefit’ in his simplified ‘rule’ for the selection pressure faced by genes on their typical inclusive fitness effects. This is known as Hamilton’s rule which, thanks to its apparent simplicity, represents the single most popular conceptualisation of inclusive fitness theory.

As suggested, the rule essentially states that, in addition to the coefficient of relatedness between the actor and recipient(s) of an act, selection will depend on the cost-benefit ratio of the act, or what Hamilton calls 'the ratio of gain' (denoted by {k} below)(Hamilton 1996 [1964], 45). Hamilton thus asks;

> "How large must {k} be for the benefit to others to outweigh the risk to self in terms of inclusive fitness?... [O]f actions which are detrimental to individual fitness, only those for which $-k>1/r$ will be beneficial to inclusive fitness. This means that for a hereditary tendency to perform an action of this kind to evolve the benefit to a sibling must average at least twice the loss to the individual, the benefit to a half-sib must be at least four times the loss, to a cousin eight times, and so on." (Hamilton 1996 [1964], 45)

The arrangement of variables in 'Hamilton's rule' can be any variation on Hamilton's notation here, so long as mathematical equivalence is maintained. Different formulations may highlight different aspects of the condition, and facilitate the understanding of the condition from a different perspective. The key point is that the calculation of 'ratio of gain' (of benefit to recipient relative to cost to actor) must supplement the value of the regression coefficient of relatedness. Hamilton's above formulation can also be stated as; the benefit (B) multiplied by the coefficient of relatedness ('r'), should be greater than the cost (C) and written; $Br>C$ or $Br-C>0$ (Hamilton 1987).

2.1.6 WHAT KINDS OF SOCIAL BEHAVIOUR?

It is important not to lose track of what Hamilton's rule refers to. As I have set out earlier in the chapter, inclusive fitness theory is best interpreted as a description of the selection pressure faced by genes on their 'social' effects. Because Hamilton's rule is simply a condition (or what he later referred to as a 'criterion', Hamilton 1987) for the evolution of social behavioural effects, potentially there are any number of different kinds of social behaviours which might meet the criterion.

We saw above that, in order for any behaviour to have a 'social' effect, the individual must express the behaviour in a context of interaction with other individuals. Only in those species whose ecology and niche lead to circumstances where individuals experience regular interaction could we expect any social behaviour effects to possibly evolve. As Sherman (1980) reminds us, inclusive fitness theory is *only relevant where the possibility for interaction exists* (note that Sherman's 'nepotism' below refers to social behaviours);

> "To understand any species' pattern of nepotism, two questions about individuals' behavior must be considered: (1) what is reproductively ideal?, and (2) what is socially possible? With his formulation of "inclusive fitness," Hamilton suggested a mathematical way of answering (1). Here I suggest that the answer to (2) depends on demography, particularly its spatial component, dispersal, and its temporal component, mortality. Only when ecological circumstances affecting demography consistently make it socially possible will nepotism be elaborated according to what is reproductively ideal. For example, if dispersing is advantageous and if it usually separates relatives permanently, as in many birds (Nice 1937: 180-187; Gross 1940; Robertson 1969), on the rare occasions when nestmates or other kin live in proximity, they will not preferentially cooperate. Similarly, nepotism will not be elaborated among relatives that have infrequently coexisted in a population's or a species' evolutionary history. If an animal's life history characteristics (Stearns 1976; Warner this volume) usually preclude the existence of certain relatives, that is if kin are usually unavailable, the rare coexistence of such kin will not occasion preferential treatment. For example, if reproductives generally die soon after zygotes are formed, as in many temperate zone insects, the unusual individual that survives to interact with its offspring is not expected to behave parentally. " (Sherman 1980, 530, underlining in original)

Many more examples and evidence illustrating Sherman's cautionary points appear in chapters four and five. The ecological niche and demographic possibilities typically occurring are *crucial* factors in an investigation of how inclusive fitness theory applies to the evolution of social behaviour characteristics of any particular species.

Furthermore, for species which display a wide range of social behaviours, such as social mammals, interactions may occur in a variety of different contexts or what Hamilton (1964, 49 see below section 2.2.2) calls "distinct behaviour evoking situations." Not all these situations will comprise the same group of recipients of a potential social behaviour. The coefficients of relationship in each situation might be quite different between interactions in the context of (for example); a sleeping nest or burrow; the local site in which the wider social group is encountered; and individuals (or groups) encountered on the peripheries of a home range, during extended foraging or migration etc. The selection pressure on the evolution of social behaviours in each of these contexts should thus be understood to vary "according to the coefficients of relationship appropriate to that situation." (Hamilton 1964, 49).

In sum, it should be clear that for a given species (whose ecological niche and demographics provide the 'potentials' for the evolution of social behaviours), there may be a range of species-typical social behaviours whose evolution can be analysed using the framework of inclusive fitness theory. Amongst these, the behaviours expressed most frequently will be those associated with the context that an individual most frequently finds itself within. Although this context may change over the life-cycle of an individual, at each developmental stage the evolution of social behaviours appropriate to the typical interaction patterns (and coefficients of relatedness) in that particular context will be shaped by selection pressure on their inclusive fitness effects. For example, at the infant stage in solitary-living mammal species, there is a fairly reliable initial grouping context; that of the reproductive female and the infant (and any litter mates).

2.1.7 CURRENT FOCUS; PRIMARY SOCIAL RELATIONSHIPS

In the current research only a limited range of social behaviours are looked at from the perspective of 'the biological facts' (see chapter 1). This narrowing of focus is necessary because potentially any behaviour that is describable as 'social' is amenable to an analysis from within the inclusive fitness theory framework. The key focus will thus be on the "behaviour evoking situations" most relevant to the study of human 'kinship'.

As suggested by the analysis in chapter one, the important question here is *what is the relationship between 'genealogy' and social behaviours*; whether an evolved behaviour must necessarily, in any given instance, lead to the expression of social bonds and cooperation between 'close genetic relatives'. I will make what I think is a reasonable assumption: If forms of social behaviour typically expressed between close relatives do not operate via identifying 'genetic relatedness' *per se;* social behavioural mechanisms typically accompanying more distant relationships (with weaker selection pressure) are not more likely to be mediated by actual identification of genetic relatedness.

This focus in the chapters ahead on the mechanisms of social bonding that have evolved due to statistical correlatation with *close* genetic relationship should not be taken as a statement that these are the only forms of social behaviour that inclusive fitness theory is applicable to. Behaviours which contribute to the survival and reproduction of larger demographic groups may be harder to analyse and define, but are in principle also treatable with an inclusive fitness theory analysis (see Hamilton 1975, below). Because the extinction (or survival) of sub-populations of species or 'groups' occurs over a much greater time scale than individual reproduction, measuring the strength of selection acting on social behaviours which have reproductive benefits for the group as a whole ('group selection') is difficult. As Eibl-Eibesfeldt puts it;

> "[W]e have to distinguish between short- and long-term effects of selection. Changes brought about by individual selection may affect fitness of a closed population in competition with others and what may be selected for in the short term by individual selection may, in the long run, lower the fitness of the group… Thus far the discussion has focused too narrowly upon short-term effects of selection." (Eibl-Eibesfeldt 1989, 93)

This potential for different selection pressures acting on the frequency of genes at different levels over different time scales is made clear by Price's treatments of inclusive fitness theory, which, as we have seen, are acknowledged (by Hamilton amongst others) to be accurate formal models. The point is, as set out above, despite some common conceptions, the theory *does not* exclude the possibility that genes promoting social behaviour receive positive selection outside the isolated interactions of close genetic relatives. Inclusive fitness theory allows for consideration of all the selective effects involved, both those arising as a result of recent common ancestry and others (Wilson & Sober 1994, Sober & Wilson 1998). Further, it is plausible that social behaviours and bonding mechanisms that initially evolve in one historical context might serve as 'exaptations' (Gould & Vrba 1982) in a later historical context, such as when group living has become so established as to make group membership necessary for survival (see also chapter 5.8). In the current research, I will be focusing on the evolution of interactions typical to 'close genetic relatives'. Hamilton clarified the potential breadth of application inclusive fitness theory in a later paper;

> "Because of the way it was first explained, the approach using inclusive fitness has often been identified with 'kin selection' and presented strictly as an alternative to 'group selection'. But the foregoing discussion shows that kinship should be considered just one way of getting positive regression of genotype in the recipient, and that it is this positive regression that is vitally necessary for altruism. Thus the inclusive-fitness concept is more general than 'kin selection'. Haldane's suggestion about tribe-splitting can be seen in one light as a way of increasing intergroup variance and in another as a way of getting positive regression in the population as a whole by having the groups which happen to have most altruists divide most frequently. In this case the altruists are helping true relatives. But in the assortative-settling model, it obviously makes no difference if altruists settle with altruists because they are related (perhaps never having parted with them) or because they recognise fellow altruists as such, or settle together because of some pleiotropic effect of the gene on habitat preference." (Hamilton 1996 [1975], 337)

Frank also sets out the generality of inclusive fitness theory;

> "Hamilton (1964a,b), in his original formulation of kin selection, described genetic similarity in terms of genes identical by descent. Hamilton (1970) reformulated kin selection by explicit derivation from the Price equation; this derivation is often regarded as the first modern treatment of inclusive fitness (Grafen 1985)… Price's covariance equation shows that what matters is not common ancestry, but statistical associations between the genotypes of donor and recipient. Those associations often arise because individuals that live near to each other tend to have common ancestors. But natural selection is indifferent to the cause of the statistical associations…" (Frank 1995, 375)

As Frank notes, it is the statistical associations between the genotypes of actor and recipient that matter. As well as inclusive fitness theory, broader analytical frameworks for the evolution of social characteristics exist (e.g. Frank 1998) that can allow for a more general analysis (for example where genealogical relationship may not necessarily be present). Nevertheless, here too, statistical association (of phenotypes) is a key component of the analysis. Inclusive fitness theory can thus be seen as one particular and well established method for studying such associations. As Frank (above) also points out, in species where these associations do arise (which always requires first and foremost that a context for interaction exists) typically the statistical association is a straightforward result of genetic relatives tending (ontogenetically) to be found near to each other. This is Frank's interpretation of inclusive fitness theory; as I have argued, it is statistical associations that are key. Is this interpretation shared by others?

2.2 PART TWO: THE INTERPRETATION AND APPLICATION OF INCLUSIVE FITNESS THEORY

2.2.1 INTRODUCTION

I have set out the basics of inclusive fitness theory as I understand it. The theory describes the selection pressure that acts on the evolution of 'social behaviours' – those behaviours expressed in the context of an interaction which impact the reproductive success of the parties involved.

This interpretation strongly rejects the idea that 'cooperation between replica genes' is a teleological goal, instead focusing on the fundamental contexts of interaction provided by the basic ecological niche occupied by a species. For social behaviours to evolve and be shaped by selection pressure on their inclusive fitness effects does not *a priori* require nor entail that organisms actively distinguish 'real genetic relatives', selection simply requires statistical associations between genotypes of donor and recipient. For example, if an individual is regularly exposed to a demographic context *typically* composed of genetic relatives, and if a gene promoting social behaviour is expressed in a way "appropriate to that situation" then the behaviour will tend to benefit replica genes. In such a case there is no need for 'positive powers of discrimination' (Hamilton 1987) of genetic relatedness. Dawkins makes a similar point in his suggestion that;

> "If families [genetic relatives] happen to go around in groups, this fact provides a useful rule of thumb for kin selection: 'care for any individual you often see.'" (Dawkins 1979, 187)

If, as Dawkins suggests, the social behaviour is cued by the social context (in this case a simple 'familiarity rule'), then the inclusive fitness criterion is achieved passively; via circumstantial cues which statistically correlate with genetic relatedness, rather than by any direct identification of genetic relatedness. Such a 'rule of thumb' can evolve because this context of relatedness is typical ('reliable') enough for the rule to meet the inclusive fitness criterion. The odd chance event by which the 'group' of interest is not in fact made up only of close genetic relatives will not significantly change the long-term selection pressures on the 'rule of thumb' behaviour.

In the following chapters I will be investigating basic demographic patterns in mammals and primates; especially those that evidence suggests are both regular and reliable, and that statistically correlate with certain coefficients of relatedness. The typical grouping context within which individuals are likely to have encountered others of particular degrees of 'relatedness' will be carefully investigated, in order to analyse the potential for *situational cues* to mediate the expression of social behaviours, and to look for supporting evidence.

The remainder of this chapter will further review Hamilton's original papers, as well as other key research on inclusive fitness theory by Grafen, Dawkins and others, including how Hamilton's ideas were interpreted, taken up and utilised by those studying social behaviour. We will note some ambiguities in Hamilton's own 1964 account, many of which were influential. Fortunately, Hamilton's later papers clarified inclusive fitness theory and even pointed out some of his own previous inaccuracies (e.g. Hamilton 1987).

The main objective in the following sections is to demonstrate that Hamilton's and other theorists' discussions of the theory strongly support the interpretation given in the first part of this chapter.

2.2.2 INTERPRETATION AS INDIVIDUAL BEHAVIOURAL ‘GOAL’ OR SELECTION PRESSURE ON GENES?

This section will review discussions bearing on whether inclusive fitness theory should more properly be interpreted as a general rule for what to expect to see in the expression of individual behaviour, or a formal description of the selection pressure on genes. The relevance of this distinction is important for an assessment of early sociobiological hypotheses (reviewed in chapter 3).

As we saw above, Hamilton’s 1964 paper was the most under-developed of his treatments of the theory and certainly, relative to his later papers, contained inaccuracies. Nevertheless, because it included a non-mathematical discussion of the possible applications of some of the theoretical points covered by the more mathematical treatment, it was this paper which had the greatest initial impact on biologists interested in studying social behaviours.

Many who subsequently subscribed to inclusive fitness theory did not pay too much attention to the underlying details of the argument, but rather took the short form of the theory - Hamilton’s rule - and used this as the guide in the analysis of animal behaviour. The rule Br>C was typically understood not simply as *a criterion describing selection pressure* on the evolution of social behaviour tendencies, but understood more directly as a guide to ‘what to expect’ of *an individual organism’s* social behaviour, without abiding the numerous caveats about ‘appearances’ and ‘circumstances’ (as set out by Hamilton 1964 and others below). In this section I will argue that this usage can lead to a completely erroneous operationalisation of the underlying theory, and thus misdirected analyses.

I have argued in the previous discussion that Hamilton’s focus was fundamentally on the selection pressures that act upon the (potentially) social effects of genes. Certainly the value of the theory for animal ethologists is the potential insight into how selection pressure has shaped the form in which social behaviours are expressed by *individual* organisms (and thus the dynamics of social behaviour within groups). But the selection pressures in fact operate on the frequencies of *genes* via their statistical ‘inclusive fitness effects’ on replicas. In truth, Hamilton’s own numerous descriptions of the potential application to the study of behaviour that his theory provides may have contributed to the emphasis on 'an individual's inclusive fitness' at the expense of considering the selection pressure on genes. He was aware that the focus of interest in his analysis would be what it meant for our understanding of the social, aid-sharing behaviour of organisms (Hamilton 1996). This dualism between pure theory and its application, perfectly understandable, nevertheless made it easy for incautious readers to oversimplify the implications of his analysis.

The following sections draw upon extracts from Hamilton's papers, and those of other theorists, to demonstrate that *the notion that individuals seek to maximise their own inclusive fitness* (a usage thoroughly reviewed in the following chapters) is erroneous. Hamilton himself conceded that certain aspects of his 1964 paper contained inaccuracies (Hamilton 1996) and later papers corrected these. One of the most important inexact suggestions ('recognition genes', see below) although not strictly an error (since it was only a suggestion) was properly corrected by Hamilton in 1987, but not before the idea had influenced the way that many people interpreted inclusive fitness theory. (This misunderstanding is perhaps the most important basis for the misplaced notion that 'individuals are selected to cooperate with genetic relatives').

Note how Hamilton presented the utility of his idea in his opening abstract;

> "A genetical mathematical model is described which allows for interactions between relatives on one another's fitness. Making use of Wright's coefficient of relationship as the measure of the proportion of replica genes in a relative, a quantity is found the means of which incorporate the maximising property of Darwinian fitness. This property is named 'inclusive fitness'. Species following the model should tend to evolve behaviour such that each organism appears to be attempting to maximise its inclusive fitness." (Hamilton 1996 [1964], 31)

The words '*appears to be attempting*' should warn us that it is *not actually* the case that organisms attempt to maximize their inclusive fitness. Even to the untrained reader, Hamilton was clear about the selection pressure on gene frequencies which underlies the evolution of these behaviours;

> "A gene causing its possessor to give parental care will then leave more replica copies in the next generation than an allele having the opposite tendency, the selective advantage may be seen to lie through benefits conferred indifferently on a set of relatives each of which has a half chance of carrying the gene in question." (Hamilton 1996 [1964], 31-32)

Particularly in his 1964 papers, Hamilton switches often between discussing the process of genetic selection and the potential behavioural traits of individual organisms. A summary paragraph at the end of Hamilton's central section 'The Model' demonstrates the distinction between the genetic model itself and its potential consequences for understanding individual behaviour;

> "Actually, in the preceding mathematical account we were not concerned with the inclusive fitness of individuals as described here but rather with certain averages of them which we call the inclusive fitness of types. But the idea of the inclusive fitness of an individual is nevertheless a useful one. Just as in the sense of classical selection we may consider whether a given character expressed in an individual is adaptive in the sense of being in the interest of his personal fitness or not, so in the present sense of selection we may consider whether the character or trait of behaviour is or is not adaptive in the sense if being in the interest of his inclusive fitness." (Hamilton 1996 [1964], 38)

Whereas the first part of the 1964 paper was more technical in focus, the second part turns to a non-technical account. However, in order that those not following the mathematical account (most readers, since, as he admitted (1996), the maths is very long-winded) should interpret his theory correctly, he makes it clear that his model is fundamentally about the selection pressures on genes;

> "In brief outline, the theory points out that for a gene to receive positive selection it is not necessarily enough that it should increase the fitness of its bearer above the average if this tends to be done at the heavy expense of related individuals, because relatives, on account of their common ancestry, tend to carry replicas of the same gene…" (Hamilton 1996 [1964], 47)

He later 'hazards' "the following unrigorous statement of the main principle that has emerged from the model";

> "The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation." (Hamilton 1964 [1996], 49)

Properly interpreted, this 'statement' gives a helpful summary of how the inclusive fitness theory can be applied to an analysis of the evolution of behaviour. Notice the word 'seem'; the individual does not in fact tailor its social behaviour depending upon the genetic relatedness of recipients as a goal; behaviours which are appropriate to the (evolutionarily typical) relatedness of individuals typically encountered in that situation/context are selected for. Hamilton, writing for a theoretical journal, could reasonably expect that readers would understand the distinction between appearances ('seems') and the fundamental process involved. Unfortunately, individual-level inclusive fitness, pursued 'as a goal' became the way many people thought about social behaviour, the shorthand way of thinking about what for Hamilton was strictly a selection pressure on '*genetic* inclusive fitness'. It was taken away in this shorthand form and applied to species behaviour 'in the field'.

In his (later written) 1963 paper he again refers, unambiguously, to selection pressures on genes and to statistical outcomes;

> "[T]he ultimate criterion which determines whether G [a gene] will spread is not whether the behaviour is to the benefit of the behaver but whether it is to the benefit of the gene G; and this will be the case *if the average net result of the behaviour* is to add to the gene pool a handful of genes containing G in higher concentration than does the gene pool itself." (Hamilton 1996 [1963], 7, emphasis added)

Overall, it should be clear, with a little caution, that Hamilton's theory concerns the selection pressures that genes face. At the same time, the ideas obviously have interesting implications for how biologists understand the evolution of social behaviours now observable in individual organisms. But the two are separate; proposed selection pressure and potential phenomena to be explained. To imagine that the phenomena itself is somehow a 'goal' of individual organisms, is to deeply misunderstand the blindness of the evolutionary process.

2.2.3 THE IMPORTANCE OF CONSIDERING TYPICAL PAST ENVIRONMENTS

I have suggested that a careful understanding of Hamilton's papers should leave no confusion as to the causal processes involved. The selection pressure relevant to what behaviours might evolve is made unambiguous in this extract from his 1971 paper;

> "The evolutionary outcome of [selection on inclusive fitness] might well be that A appeared in his social behaviour to value his relative's fitness against his own according to weightings given by [the regression coefficient of relatedness]. He would always value a unit of fitness in a relative less than a unit of his own fitness except in the special case in which the individual is clonal (as in the case of an identical twin): then [the coefficient] = 1. In humans, twinning is too rare for any special social adaptations to have arisen upon this relationship…" (Hamilton 1996 [1971], 210)

This point about the rarity of twinning in humans demonstrates that a *particular instance* of an association of replica genes (in this case a coefficient of relatedness of 1.0) is irrelevant to consideration of the *evolution of* behavioural propensities. If one is interested in analysing a species-typical behaviour, an analysis of the *typical past* selection pressures on the genes that constitute the species is key. Neither genes nor individuals should be assumed to pursue *goals* of inclusive fitness maximisation nor actually 'value' other individuals' fitness on the basis of their actual genetic relatedness *per se*. A consideration of the typical social encounters regularly occurring in past environments is obviously necessary, and therefore a consideration of typical demographic patterns and such like.

Dawkins (1979) makes a very similar point about the relevance of *past* selection pressures in his paper about common misunderstandings of Hamilton's theory. Under the common misunderstanding labelled 'Altruism is necessarily expected between members of an identical clone', he notes that;

> "There are races of parthenogenetic lizards the members of which appear to be identical descendents, in each case, of a single mutant female (Maynard Smith 1978). The coefficient of relatedness between individuals within such a clone is 1. *A naïve application of rote-learned kin selection theory* might therefore predict great feats of altruism between all members of the race. [This misunderstanding is] tantamount to a belief that genes are god-like. Genes for kin altruism spread because they are especially likely to help copies of themselves rather than of their alleles. But members of a lizard clone all contain the genes of their original founding matriarch. She was part of an ordinary sexual population, and there is no reason to suppose that she had any special genes for altruism. When she founded her asexual clone, her existing genome was 'frozen', a genome that had been shaped by whatever selection pressures had been at work before the clonal mutation." (Dawkins 1979, 193, emphasis added)

This passage emphasises that expression of positive social behaviours is not a goal of individuals or genes. The selection pressure on inclusive fitness that genes are subject to is dependent on the existence of 'potential' - a reliable context of interaction. This means that genes and behaviours that are now species typical must be understood to have evolved in past environments, and the effects of their expression in any given current instance can only reflect selection pressures in typical past environments.

2.2.4 WHAT KINDS OF BEHAVIOUR AND WHAT KINDS OF SITUATION?

This brings us on to another commonly misunderstood aspect of inclusive fitness theory, particularly by those involved in early attempts to apply it to humans.

If one is analysing a behaviour which is taken to be 'species-typical' at the time of analysis, the selective context under which that behaviour has evolved is the sum of all past environments that the genes and the behaviour have been expressed in. In reality this is obviously an indefinitely long backwards extending continuum, and is not directly observable.

However, the relevant selective environments may be indirectly hypothesised by making assumptions about the similarities and differences between the species' current environment (or ecological niche) and those of the past. Comparison between observable fundamental demographic patterns of closely related species may also assist in this investigation.

We have seen that in any particular species 'social behaviour' can take many forms, be expressed in narrower or wider demographic contexts, and involve different levels of cost and benefit to actors and recipients (see above section 2.1.5). What kinds of social behaviour did Hamilton himself consider would most straightforwardly reflect the selection pressure on social behaviours suggested by his theory? In this section we will consider some of Hamilton's suggestions, as well as those of other related theorists. Remember Hamilton's summary statement;

> "The Social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation." (Hamilton 1964 [1996], 49)

To put our question differently, which behaviour-evoking situations (with what typical coefficients of relationship) might best reflect selection pressure on inclusive fitness effects? Unfortunately, there were one or two inconsistencies in Hamilton's own initial discussion of these possibilities, which led to a great deal of later confusion (see below). However, his own suggestions included the following;

> "Tinbergen investigated the ability of herring gulls to recognise their own chicks by observing their reaction to strange chicks placed amongst them. He found that during the first 2 or 3 days after hatching, strange chicks are accepted, but by the end of the first week they are driven away… During the days which follow hatching, the chicks become progressively more mobile and the chance that they will wander into neighbouring nest-territories must increase. Therefore it seems a reasonable hypothesis that the ability to discriminate 'own young' advances in step with the chance that without such discrimination strange chicks would be fostered and the benefits of parental care wasted on unrelated genes. Supporting this hypothesis are the findings quoted by Tinbergen of Watson and Lashley on two tropical species of tern: 'the Noddies nesting in trees do not

> recognise their young at any age, whereas the ground-nesting Sooties are very similar to herring gulls in that they learn to recognise their own young in the course of four days.' House sparrows will accept strange young of the right age placed in the nest but after the nestlings have flown 'they will not, in normal circumstances, feed any but their own young.'" (Hamilton 1996 [1964], 53-54)

Tinbergen's work was a cornerstone of the field of ethology, along with that of Konrad Lorenz. Both studied mechanisms of bonding operating in early development, as would typically occur between parent and offspring, illustrated here by Tinbergen's work on gulls. Ethologists' work on 'imprinting', the mechanism whereby infants typically attach to a parent has also been influential in studies of attachment mechanisms operating in mammals and primates, as will be discussed in later chapters. Hamilton here focuses on social bonding that occurs in particular and reliable contexts; he suggests that social behaviours could reliably meet the inclusive fitness criterion if circumstantial cues that *tend to correlate with genetic relatedness* mediate social bonding.

As we saw above, Dawkins makes a similar point to Hamilton; that social behaviours can be mediated by straightforward contextual rules of thumb;

> "Animals cannot, of course, be expected to know, in a cognitive sense, who their relatives are, and in practice the behaviour that is favoured by natural selection will be equivalent to a rough rule of thumb such as 'share food with anything that moves in the nest in which you are sitting.' If families happen to go around in groups, this fact provides a useful rule of thumb for kin selection: 'care for any individual you often see.'" (Dawkins 1979, 187)

Following on from Hamilton and Dawkins, what have other theorists suggested about the mechanisms by which genes might statistically 'track' their replicas? The following section takes up this question.

In sum, both Hamilton and later inclusive fitness theorists like Dawkins suggest that social behaviours that meet the inclusive fitness criterion can be mediated by cues such as context and familiarity. To the extent that social behaviours can be contextually cued, this further highlights the importance of considering the typical past demographic patterns relevant to a species; later chapters conduct such an analysis (chapters 5 and 6).

2.2.5 "TRACKING RELATIVES" BY CONTEXT OR POSITIVE POWERS?

In this final section of chapter two, we conduct a brief review of what inclusive fitness theorists have said about possible mechanisms which statistically correlate social behaviour with genetic relatedness ('track relatedness'). This introduction will enable the reader to assess the validity of sociobiological hypotheses applied to humans, reviewed in the next chapter (chapter 3). This is a fairly complex area and a fuller analysis of what mechanisms do appear to operate in the human case will be conducted in chapters four to seven. This section thus serves as a brief introduction to some of the issues.

In the following passage Hamilton (1964), whilst demonstrating his now familiar 'shorthand' use of the individual perspective to illustrate potential behaviours (see discussion, section 2.2.2), further emphasises the context of social behaviours and the need to consider which individuals the behaviour benefits. However, Hamilton also introduces the suggestion that behaviours which achieve the necessary 'bias' towards relatives via 'recognition', might do this either via 'active recognition' or circumstantially;

> "The selective advantage which makes behaviour conditional in the right sense on the discrimination of factors which correlate with the relationship of the individual concerned is therefore obvious. It may be, for instance, that in respect of a certain social action performed towards neighbours indiscriminately, an individual is only just breaking even in terms of inclusive fitness. If he could learn to recognise those of his neighbours who really were close relatives and could devote his beneficial actions to them alone an advantage to inclusive fitness would at one appear. Thus a mutation causing such discriminatory behaviour itself benefits inclusive fitness and would be selected. In fact, the individual may not need to perform any discrimination so sophisticated as we suggest here; a difference in the generosity of his behaviour according to whether the situations evoking it were encountered near to, or far from, his own

> home might occasion an advantage of a similar kind." (Hamilton 1996 [1964], 51)

A contextual rule of thumb which causes a social behaviour to tend to be expressed 'near the home', rather than far from it is clearly of the type discussed by Dawkins and Hamilton in the previous section. But what sort of more 'sophisticated' forms of possible discrimination did Hamilton have in mind? Following his discussion of the circumstantial rule of birds feeding young in their own nest (previous section), Hamilton makes a further point;

> "In situations where the relationship is not variable, for example, between the nestlings in an arboreal nest, there remains a discrimination which, if it could be made could greatly benefit inclusive fitness. This is the discrimination of those individuals which do carry one or both of the behaviour causing genes from those which do not. Such an ability lies outside the conditions postulated in Part I [his mathematical treatment] but the extended meaning of inclusive fitness is obvious enough. That genes could cause the perception of the presence of like genes in other individuals might sound improbable; at simplest we would need to postulate something like a supergene affecting (1) some perceptible feature of the organism, (2) the perception of that feature, and (3) the social response consequent upon what was perceived." (Hamilton 1996 [1964], 54)

It is this supplementary suggestion about what have come to be called 'recognition genes' which has been influential in what Dawkins (1979, above) referred to as "*naïve applications of rote-learned kin selection theory*". It is likely that Hamilton did not work through these possibilities very thoroughly before making this suggestion in 1964, since he himself would later come to effectively withdraw the suggestion and point out other reasons why such a gene would in fact be unlikely to evolve (Hamilton 1987, see below), particularly in the context of interactions between individual organisms of a diploid species. Such 'recognition genes' could evolve without modification in the context of interactions between clonal cells in a multi-cellular body.

It is important to note that direct genetic-level recognition of relatedness between individual organisms is *not* a prediction of inclusive fitness theory. Even at the time of his initial mentioning it, Hamilton himself makes this clear when he says that this is an 'extended meaning' of inclusive fitness "lying outside the conditions postulated in part I" (the first, theoretical part of the 1964 paper). I classify the idea - that 'recognition genes' *will evolve* as a consequence of inclusive fitness theory - as a teleological error of the type already discussed. As we will see below, Hamilton's 1987 treatment clarifies that recognition genes are in fact in principle extremely unlikely to be sustained by natural selection.

Nevertheless, I discuss Hamilton's notion here, because this extended interpretation of the possible implications of inclusive fitness theory (and similar interpretations) have become very commonplace, and have unfortunately obscured both the fundamentals of the theory and obscured the more simple behavioural mechanisms whereby *genes* might effectively 'track' their likely replicas. We have seen that genealogical relatedness is considered the most straightforward factor producing the necessary reliable statistical association at the genetic level required for a social behaviour to evolve. Other possibilities ostensibly exist, in principle, such as 'recognition genes' or pleiotropic genes which also cause a habitat preference such that those that bear them tend to congregate and differentially interact. Grafen (1984) makes clear why the sustained presence of such genes would be unlikely;

> "The other way for r [the regression coefficient of relatedness] to be raised in groups besides common ancestry is preferential assortment. If altruists share a preference for certain micro habitats, then altruists will tend to be in groups with other altruists and that is all that is required to make r positive according the definition above. There are a number of reasons why preferential assortment is not a plausible source of genetic similarity in nature. They are based on the fact that while common ancestry provides relatedness that is the same for all loci, preferential assortment only causes relatedness that is the same at the loci that cause it and at closely linked loci. It is unlikely that the locus for altruism is closely linked to the loci for habitat preference. Even if it were, there would be selection at unlinked loci to suppress the altruism; for while the r at the altruism locus may be positive, the r at unlinked loci is zero and Hamilton's rule applies equally to both sorts of loci. Finally there would be selection for a 'free-rider' allele (if one arose) at a locus unlinked to the altruism locus. It would have the effect of creating the same habitat choice as the altruists, whether or not its bearer was an altruist. For all these

> reasons, the only plausible cause of genetic similarity between group members is common ancestry." (Grafen 1984, 79)

Maynard Smith (1976) makes a relevant point in his discussion of the conditions under which we might usefully consider behaviour to have evolved via 'group selection' rather than at the level that he (Maynard Smith 1964) labelled 'kin selection' (in deliberate contrast to group selection);

> "If, for example, animals behave with an equal degree of altruism to all their "neighbours"… and if *on average* animals are related to their neighbours, then I would regard this as an example of kin selection. It is not a necessary feature of kin selection that an animal should distinguish different degrees of relationship among its neighbours, and behave with greater altruism to the more closely related…" (Maynard Smith 1976, 282, emphasis in original)

Maynard Smith continues;

> "Apart from relatedness, there are other possible reasons why members of a [group] might resemble each other genetically. If individuals of like genotype tend to associate together, either because they are attracted to one another, or because they are attracted by common features of the environment, or because they are survivors of a common selective force, then altruism can be selected for. Before invoking this mechanism, however, it is important to remember that if an altruistic allele *a* is to replace a selfish allele *A,* then the members of a trait-group must resemble one another *at that locus*. If they are not related in the normal sense, this would require that the altruistic locus have pleiotropic effects determining association. Thus, these other reasons for genetic similarity between neighbours seem likely to be unimportant compared by identity by descent." (Maynard Smith 1976, 282, emphasis in original)

Again, these points made by Maynard Smith and Grafen are relatively easily understood if the distinction between genes and individuals is kept clear. 'Kin' (here explicitly used to mean genealogical relatives) are, on average, equally related at all loci consistently, generation after generation, such that *all* genes (at all loci across the genome) face equal selection pressure on their inclusive fitness effects. A 'recognition gene' might possibly be able to evolve the necessary components to signal, recognise and trigger a social behaviour, especially if we allow that a few tightly linked genes might achieve this effect. However, it remains the case that whilst such a gene would be prompting the individual to identify and bias social behaviours towards individuals with replica genes at this locus, by definition all other genes in the actor would be suffering a 'fitness cost'. There are a number of other ways to consider why such 'recognition alleles' would in fact be very unlikely to evolve effects of the sort hypothesised, all of which require a clear understanding of the details of inclusive fitness theory. This leads Dawkins who had previously (1976) dubbed recognition alleles as 'Green Beard genes' to comment that;

> "Some of the suggested [genetic] outlaws that I shall now come to are, frankly pretty improbable. I make no apology for this. I see them as thought experiments. They play the same role in helping me think straight about reality as imaginary trains travelling at nearly the speed of light do for physicists… The green beard effect is not a mechanism for the recognition of kin. Rather, kin recognition and 'green-beard' recognition are alternative ways in which genes could behave as if discriminating in favour of copies of themselves… [I]t is clear that genes mediating altruism towards close kin, and favoured by conventional kin-selection pressure, are definitely not outlaws. All the genes in the genome have the same statistical odds of gaining from the kin altruism behaviour, for all have the same statistical odds of being possessed by the individual benefited. A 'kin-selection' gene is, in a sense, working for itself alone, but it benefits the other genes in its genome as well. There will therefore be no selection in favour of modifiers [other genes] that suppress it." (Dawkins 1999 [1982], 143-149)

Dawkins concludes thus;

> "The green-beard effect may be implausible, but it is instructive. The student of kin selection who first understands the hypothetical green-beard effect, and then approaches kin selection theory in terms of its similarities to and differences from 'green beard theory', is unlikely to fall prey to the many tempting opportunities for error that kin selection theory offers (Dawkins 1979a). Mastery of the green-beard model will convince him that *altruism towards kin is not an end in itself*, something that animals are mysteriously expected to practice in accordance with some clever mathematics that field workers don't understand. Rather, kinship provides just one way in which genes can behave as if they recognised and

> favoured copies of themselves in other individuals. Hamilton himself is emphatic on this point…" (Dawkins 1982, 153, emphasis added)

Dawkins goes on to quote Hamilton's point that inclusive fitness theory is more general than 'kin selection' (Hamilton 1975, see section 2.1.7). Grafen makes some similar points in his (1990) discussion of some of the conceptual problems accompanying 'kin recognition' theory;

> "The requirements for genetic similarity to select consistently for altruism are first, continuing similarity in time as gene frequencies change and the altruistic trait spreads through the population; and, second, the similarity must hold through a large enough fraction of the genome, as it must be expected that modifiers will arise at distant loci. These conditions are not met by the local and transient additional similarity imposed by the process of ['green-beard'] matching at the matching locus itself." (Grafen 1990, 53)

Hamilton's thoughts on this become more clear as in his later papers, and he specifically discussed these matters in a 1987 paper, this time with further deliberations accompanied by conclusions in line with what other theorists (such as the others in this section) have suggested;

> "[S]uppose that a root connection is made [between two trees] and that subsequently one tree is dying for want of water, to which the other has limited access. Suppose the other supplies the dying tree with water at a benefit-for-cost ratio far more generous than the limit set by the kin selection criterion [Br>C] based on pedigree relatedness. The helping tree as a result sets less seed and the helped tree sets more seed – but the 'more' is not enough to fulfil the criterion except at the recognition locus and possibly at loci very nearby. Suppose this happens again and again in instances of such paired trees. If now, elsewhere in the genome, a mutant gene arises that blocks the outward sap flow at this benefit-for-cost ratio, then that gene is advanced. This is easily seen by the kin-selection principle. Thus as regards its action as a potential donor, the genome evolves to suppress a 'green-beard' transfer. Effects of this kind would therefore be transitory and be unable to evolve into regular adaptations. If such aid is given regularly through root grafts, it is likely to be established on some basis either of typical kin selection or else of reciprocation." (Hamilton 1987, 421, 424)

It is interesting to note (as *per* Dawkins 1982) that a purely individual-level interpretation of inclusive fitness theory would be inadequate to analyse the selection pressures at work in such cases, and Hamilton's use of a gene and genomic level perspective on the selection pressure described by the inclusive fitness criterion [Br>C] here is unambiguous.

2.3 SUMMARY

This review and discussion has demonstrated some of the means by which biological theory throughout the 20th century has sought to develop models for understanding the *evolution* of social behaviours consistent with foundational biological models (*the modern synthesis*). The prominent model for the evolution of certain forms of social behaviour is *inclusive fitness theory*. Specifying one necessary criterion for the *evolution* of social traits involving a statistical association between replica genes, correctly interpreting this theory needs to be approached cautiously. If ecological conditions that promote social grouping are reliably present in a species' evolutionary history (rare in mammals beyond weaning), and potential social traits arise in the gene pool, the inclusive fitness criterion specifies the selective conditions for their increase in frequency (evolution). The relevance of 'genetic relatedness' is that *common ancestry* provides one particularly reliable degree of genetic correlation between individuals, via which the necessary criterion of statistical covariance of replica genes with reproductive fitness may be fulfilled.

Being a general theory about selection pressures acting upon the *evolution* of social traits, the particular *proximate* mechanisms of a potential social trait cannot be formally specified by the theory, although Hamilton voiced some possibilities. Since an ecological context that provides for social interaction is a prior necessary condition, then location-based and *context-based cues* are parsimonious candidates for proximate mechanisms of social behaviour compared to *'positive powers'* of identifying genetic relatedness via active *'kin recognition'* mechanisms. This debates will be treated in more detail in chapter four. Chapter three reviews how sociobiological hypotheses *claiming to represent* inclusive fitness theory have been applied to humans.

CHAPTER THREE – SOCIOBIOLOGICAL TREATMENTS OF KINSHIP

3.01 INTRODUCTION

This chapter reviews a number of past treatments of human social behaviour which have been advanced in reference to evolutionary biology theories. As suggested at the end of the first chapter, the approaches of most interest are those of sociobiology, in particular the 'Darwinian anthropologists', who have explicitly approached the subject in reference to an interpretation of inclusive fitness theory. I will argue that the interpretation of the theory utilised in these approaches is erroneous.

Other schools drawing on biological theory in application to human behaviour include evolutionary psychology as well as gene-culture 'Dual Transmission' theories. The latter, including work by Cavalli-Sforza and Feldman (1981), Richardson and Boyd (2001) Lumsden and Wilson (1983) and others, mainly focus on the co-evolution of genes and culture, and have not attempted to apply inclusive fitness theory to individual human social behaviours specifically (Hewlett 2001). For this reason the current review will not discuss gene-culture models. Evolutionary psychology has officially adopted a different emphasis from Darwinian anthropology, especially an investigation of proximate mechanisms and, in a sense, the school stemmed from a critique of Darwinian anthropology's interpretation of inclusive fitness theory, which will be discussed below. However, in general evolutionary psychology has not paid particular attention to individual social behaviour or broader patterns of social interaction in a wide diversity of societies (Hewlett 2001); the areas of traditional interest to anthropology. The exceptions here are Daly and Wilson (Daly et al. 1997), whose work was briefly sampled in chapter one (section 1.6), and whose rare excursions in to anthropology essentially repeat the claims of the Darwinian anthropologists reviewed here (see section 3.5)

In reviewing the early Darwinian anthropology treatments of human social behaviour, the focus here is on the premises (section 3.2) of their positions which demonstrate the misinterpretations first discussed in chapter two. First however, an overview is given of the genesis of Darwinian anthropology and the various derivative treatments.

3.02 DARWINIAN ANTHROPOLOGY - OVERVIEW

In the 1970s and 1980s a number of attempts were made to apply new insights about the evolution of social behaviour derived from inclusive fitness theory to certain classificatory ethnographic phenomena described by anthropologists and comparative sociologists over the previous hundred years (see chapter 1). In particular, explanations were offered for 'kinship' patterns; unilineal descent (matrilineal and patrilineal descent groups), and phenomena such as the avunculate (the 'mother's brother'). These Darwinian anthropology approaches all followed essentially the same format and assumptions, and were initiated by Richard Alexander's early paper discussing potential application of inclusive fitness theory (here conceptualised as 'kin selection') to human data (Alexander 1974; Greene 1978; Kurland 1979; Irons 1979; Gaulin & Schlegel 1980, Flinn 1981, Hartung 1985).

As noted in the first chapter, these analyses suffered a number of problems. The tradition in anthropology for conceptualisations of human social behaviour as large scale structural phenomena (e.g. descent theory) was on a downhill slope, if not quite redundant (see chapters 8 and 9). Nevertheless, had the analyses been productive, this would not have mattered and the approach may have attracted interest. The greater difficulty was that these approaches mistook the anthropological class 'kin' with its namesake in biology and attempted to translate 'kin' into 'genetic relative' by suggesting that human social interactions always reflect individuals' attempts to maximise their own individual 'inclusive fitness'.

We saw in chapter two that this 'individual goal' interpretation of the theory is problematic. Biologists themselves (Dawkins 1976, Gould & Lewontin 1979, Kitcher 1985) have been critical of some interpretations of inclusive fitness theory, including the Darwinian anthropology approach. Kitcher's criticism in particular targeted these attempts to explain human kinship patterns for (as he saw it) an over-reliance on the existence of a hypothesised 'general purpose mechanism' of individual inclusive fitness 'maximisation', in addition to pointing out shortcomings in explaining the empirical details. The latter part of this chapter (section 3.5 below) will review Kitcher's critique and his suggestion of the need to focus on intermediating (or 'proximate') psychological or behavioural mechanisms.

Other biologists who strongly believe that human behaviour is amenable to evolutionary biological analyses also criticise Darwinian anthropology approaches to applying inclusive fitness theory to humans (Symons 1989). The main criticism here resembles that of Kitcher; this approach assumes that individuals continue to maximise their "individual inclusive fitness" in all present environments, whilst ignoring analysis of evolved mechanisms that selection pressure has acted on in past environments. This is the position taken up by evolutionary psychology, but it is not clear that this school actually advances hypotheses about human social behaviour that differ from those of the Darwinian anthropologists (section 3.5).

3.03 SUMMARY OF CRITIQUE

For clarity I here set out the 'errors' of early Darwinian anthropology, many of which have been introduced in chapter two. Section 3.2 (below) will attempt to illustrate these errors by examples from the treatments.

Firstly, as suggested above, these approaches understood inclusive fitness theory to imply that *individuals* will behave in a way which maximises 'their inclusive fitness'. We saw in chapter two that this is necessarily a simplified interpretation of the theory, and that any reference Hamilton made to individual inclusive fitness was intended as a guide to the other-things-being-equal "appearances" of behaviour (*evolved* tendencies tuned to typical features of past environments). The theory implies simply that genes face selection pressure to have effects which, in the environments in which they have existed (always *past* environments from the point of view of *current* behaviour) by-and-large meet the inclusive fitness criterion.

Secondly, Darwinian anthropology, in taking the *individual* level perspective made theorists particularly prone to forms of anthropocentrism; particularly in interpreting inclusive fitness theory to involve 'male interests' or sometimes 'female interests', for what is correctly the evolutionary selection pressure on genes which (except the Y chromosome and cytoplasmic genes) pass through both sexes in mammals. (Hartung's work (reviewed below) is an interesting case in point here, since he initially did focus on selection pressure on genes (1976), but later used an individual-level perspective (1985), and since has regretted this step (1997)). Further, the individual perspective involved certain assumptions about the universal evolved behaviour of human males (ardent) and females (coy). This influenced further assumptions about proposed (evolved, species-typical) bonding norms between males and females, and thus 'normal' connections between a male and 'his offspring', reinforced by a limited perspective apparently derived from monogamous cultures. These perspectives led to the assumption that human males have long been selected to achieve individual inclusive fitness by investing in 'their offspring' (referred to as 'Male Parental Investment') in a way assumed to be qualitatively equivalent to female-offspring interaction.

It should be clear from chapter two that - even if we accept for the moment, for the sake of argument, an 'individual' interpretation of inclusive fitness theory - equivalence between 'what is expected' of males and females can only be valid if evolutionarily-typical 'grouping contexts' of interaction between male-and-offspring and female-and-offspring are correspondingly symmetrical. This position is unsustainable alongside the evidence from mammals (see chapters 4 to 6).

Further, in making the assumption that 'individuals maximise their inclusive fitness', Darwinian anthropology regarded the actual intermediating 'proximate' behavioural mechanisms of social behaviour as a "black box"; operating via an unexamined general purpose mechanism (see Kitcher section 3.5). Surprisingly, this remains the case with evolutionary psychology treatments of anthropological 'kinship' data. As was suggested in chapter two, misunderstanding this point led crucially to a misplaced assumption that 'kin discrimination' must be somehow unerring and achieved precisely, rather than meeting the inclusive fitness criterion via behavioural mechanisms sensitive to mediating cues *that have typically in past environments correlated with genetic relationship*. Kitcher makes the point that the operation of such 'proximate' behavioural mechanisms might actually be straightforward (see section 3.6).

The current research will investigate the possibilities for the operation of such mechanisms by considering likely demographic features of evolutionarily significant environments, not simply by considering those evolutionary environments unique to humans, but more fundamental demographic conditions relevant to closely related species also (see chapters 4 to 6). As well as paying little attention to ethnographic evidence and anthropological perspectives, Darwinian anthropology did not generally benefit from comparative primatological evidence, which was particularly surprising for an approach grounded in evolutionary biology. The deep evolutionary history of mammals and primates, and demographic factors such as the evolutionarily typical 'grouping contexts' of female-plus-infants and maternal-siblings was not considered relevant. One notable exception was Kurland (1977) who had in fact investigated social behaviours in primates, but not with a view to the variables recommended here (since his interpretation of inclusive fitness theory was different), and he thus saw no similarities to evolved human behaviours.

3.1 DARWINIAN ANTHROPOLOGY

3.1.1 GENESIS AND CORE HYPOTHESES

Richard Alexander (1974, 1979) was one of the first to suggest ways in which inclusive fitness theory might be applicable to human social behaviour, particularly in relation to some long standing phenomena traditionally studied by anthropologists. His 1974 paper provoked a number of other treatments whose aim was to recast various aspects of human behaviour in terms of "individual inclusive fitness maximisation" and this school soon came to be referred to as Darwinian anthropology. Fox (1996), for example, gives this account;

> "Largely under the influence of Alexander (1974), a school of sociobiological thought emerged which took as is central precept the maximisation of reproductive success. Its main assumption is that such maximisation… can explain a whole range of human mating and kin-related behaviours." (Fox 1996, 814)

Alexander was working on these ideas some time prior to his 1974 paper, and his influence on others is illustrated by John Hartung;

> "It was December of 1972 and I went on my motorcycle. Just as I thawed out, about fifty minutes into his talk, R.D. Alexander explained mother's-brother's-sister's-son. There was hope." (Hartung, in Betzig 1997, xiii)

Clearly Alexander's ideas stimulated interest in investigating some of the patterns of social behaviour that anthropology had long been describing, notably areas of what anthropology had called 'kinship' (see chapter 1). Alexander had raised a number of possibilities - his paper is wide ranging and touches on a large number of general issues raised by the application of Hamilton's theory to animal behaviour. His starting position regarding the application of inclusive fitness theory to human social behaviour is that;

> "Although human societies are groups of variously related individuals within which genetic relationships are universally rather well understood, a more or less general rejection by social scientists of the idea that nepotism is related to the reproductive history of humans has stifled attention to the correlations between genetic relationship and the likelihood of altruism." (Alexander 1974, 372)

Alexander goes on to discuss cousin marriages from the perspective of a balance between inbreeding and outbreeding (Alexander 1974, 373), and then continues;

> "Similarly, the phenomenon of "mother's brother" as the adult male responsible in certain ways for some children is at least sometimes prominent in polygynous societies in which confidence of paternity is quite low. Low confidence of paternity may result from (for example) living arrangements; as an extreme case wives may live separately from husbands… Genetically speaking, a man's sister's offspring are on the average ⅛ to ¼ like him… his spouse's offspring, on the other hand, may be ½ like him or (depending on her fidelity) totally unlike him. As confidence of paternity diminishes, therefore, a man's sister's offspring become relatively more important to his reproduction, and a woman's brother becomes a more likely candidate for parental behaviour for her offspring that may otherwise suffer from a lack of paternal assistance." (Alexander 1974, 373)

This initial hypothesis of Alexander's formed the basis for a number of subsequent research efforts. Implicit in this perspective (and many later developments of it) are a number of assumptions. There is the assumption that (universally) males' levels of confidence about paternity are a centrally important influence on social organisation. The perspective assumes that patterns of bonding between males and females 'usually' have a certain character; that they are 'spouses' to each other and that offspring of the female are 'normally' offspring of the male she is with 'depending on her fidelity'. Subsequent Darwinian anthropologists (reviewed below) partially recognised that this was a highly limited perspective on the norms of male-female bonding in humans. Alexander's hypothesis also assumed that the default behaviour of a human male (given the relatedness correlates of the 'normal' male-female bond) is to 'parentally invest' (Trivers 1972), and that normal human infants would suffer from a lack of *paternal* assistance. A derivation, not made explicit by Alexander is that the avunculate should be correspondingly absent in 'high confidence of paternity' societies, where according to his position males 'should be' investing in their wives' offspring (in the knowledge that these are their own offspring).

It is equally possible that many of these premises about supposedly sex-specific evolved dispositions are in fact derived from a particular view of the 'family man' gender role of males in Euro-American culture. Indeed, this suggestion is in fact made by one of the Darwinian anthropology treatments (see quote from Irons 1979, section 3.2.4 below). These premises resemble the 'man the hunter' concept (see section 1.3.2) which includes the idea of a male's contribution to child rearing, also known as the 'hunting hypothesis' (Hawkes et al. 2000, Hewlett 2001);

> "[T]his hypothesis suggests that many aspects of human social organisation (patrilocality, sharing, monogamy, nuclear family) were consequences of big game hunting. Males hunted game to provide for the nuclear family; from a life history perspective, they were investing energy into male parental effort." (Hewlett 2001, 101)

Chapter one reviewed critiques of this idea, which cited evidence from primate species in which the female (and maternal relatives) rear infants without male assistance (see 1.3.2). More recent evidence (reviewed in section 3.2.2), also supports the view that many of the assumptions of this hunting hypothesis may be unsafe.

Nevertheless, these possibilities discussed by Alexander were taken up and developed by a number of later researchers in the 1970s and 1980s. These treatments assumed the validity of Alexander's basic idea, and thus relied on a similar set of assumptions about the deep roots of 'male parental investment' in human nature, and the norms of bonding between males and females. The first section below is restricted to a brief overview of how Alexander's idea was developed through to Hartung's 1985 paper, after which these treatments tailed off (but see Daly and Wilson, section 3.5). The following section then identifies and critiques in more detail the assumptions and premises of this Darwinian anthropology approach in general, as outlined in the first chapter, many of which continue to underlie proclaimed 'evolutionary biology' treatments of human behaviour.

3.1.2 DARWINIAN ANTHROPOLOGY DEVELOPMENTS OF ALEXANDER'S HYPOTHESIS

The common theme running through all the extensions of Alexander's hypothesis is the attempt to reformulate the initial premise about a male's genetic connection to his wife's offspring into a form that might account for the relatively common incidence of avuncular relationships documented in ethnographic accounts. Under the original formulation, a man would only do better to invest in his sister's offspring when his 'certainty of paternity' (the chance that he is the actual genetic father) is below the 'paternity threshold' of approximately 0.265 (a wife's child is actually his child only approximately ¼ of the time). In reality - and what Alexander had apparently not appreciated in the 1974 paper (but had by 1979) - the avuncular relationship occurs not only when paternity is comparatively uncertain, but also when "it is practically certain" (Fox 1985, 675) as had long been appreciated by anthropologists and comparative sociologists (reviewed below, section 3.2.3). Thus the emphasis in subsequent Darwinian anthropology treatments on progressively redefining of their 'paternity threshold' in ways that make it closer to realistic 'levels of paternity' in the societies in question. This section follows the developments of the ‘internal logic’ of the basic hypothesis in these treatments, emphasising the continuities between them. Most clear is their focus on ‘true genetic relatedness’ as the organising force for social patterns.

The first published reworking of Alexander’s idea was that of Greene (1978), although Kurland was conducting related work at the same time, published slightly later as a book chapter (Kurland 1979). Greene discusses inclusive fitness theory and Alexander’s suggestions about the avunculate, and introduces an element that (what she calls) the ‘Alexander-Kurland model’ doesn’t distinguish. She suggests that placing a value on ‘uncertainty of paternity’ derived from the proportion of the time that a woman’s husband is actually the biological father does not necessarily give a full account of the ‘genetic relatedness’ of the situation. Alexander and Kurland’s treatments had incorporated the diluted ‘relatedness’ between a (maternal) brother and sister due to *their own* common paternity being ‘uncertain’. Greene suggests that this need not be the case because there is a chance that females in such societies may be ‘consistently unfaithful’ with the same one male (or with closely related males), and therefore that the brother and sister in the ‘avunculate’ may themselves be related. This degrees-of-relatedness tinkering allows the ‘paternity threshold’ below which the avunculate ‘makes sense’ to be adjusted up by a few percentage points, towards levels that appear less unrealistic against the ethnographic record.

Kurland’s (1979) treatment takes in the point about low certainty of paternity also affecting the brother-sister relatedness, and finds a “probability threshold” of 0.268 below which a man should invest in his sister’s children. Kurland admits that this seems low compared to ethnographic reports, and that the avunculate is prominent at levels above this. Like Greene, Kurland has a ‘work around’ and suggests that in societies where marriages are serial and paternity probability is low, a wife’s household may consist of a number of children who are *known* to be unrelated. The probability threshold should thus be interpreted as the chance that a given child of the wife is the child of the male doing the investment and this probability will be affected by previous reproductive history. If the nature of that investment means it cannot be directed to specific children in the wife's 'brood' ('non-partible investment'), Kurland suggests, a male should be expected to preferentially invest in his sister's children. Essentially, Kurland is adjusting the Darwinian anthropology claim by suggesting that societies in which the avunculate is prominent may regularly feature female-orientated families in which maternal siblings are (unambiguously) the products of a series of relationships the female has had with males over her reproductive career. This is an interesting suggestion but one which, in essence, introduces a quite different set of assumptions about the strength of typical spousal bonds between males and females.

Even though these possibilities concerning variable spousal bonding 'norms' are logically required to be a feature of human societies for the overall argument to work, they are simultaneously not allowed to challenge the fundamental Darwinian anthropology assumptions on the norms of human nature. That is, the central issue (and major premise) continues to be - males' purportedly evolved desire for significant parental investment in *their own genetic offspring* (to maximise their 'individual inclusive fitness'), and the hypothesis remains that social cooperation amongst matrilineal relatives (including the avunculate) *arises because of* low probability of paternity. Further Darwinian anthropology assumptions about dependent and independent variables are discussed in a later section.

In the same edited volume as Kurland, Irons (1979) also discusses many of the same features of human societies, drawing on Darwinian anthropology theory, and refers to the three treatments discussed so far;

> "As long as paternity certainty is less than perfect, a man is more closely related to a sister's children than to a brother's children… Kurland (chapter 6) discusses how low paternity probability diminishes average relatedness through all male links, and thus shifts the optimal recipients of kin effort. The effect of paternity probability is especially relevant to the issue of Nayar men investing in the sister's children rather than the wife's (i.e. *sambandham* partner's) children. Greene (1978) has shown that men will be on average more related to sister's children than to wives' children if paternity probability falls below a value of 2 – 3½ or approximately 0.268." (Irons 1979, 189)

Gaulin and Schlegel (1980) define paternal confidence as the 'probability that a man is genitor of his wife's children' (Gaulin & Schlegel 1980, 302) thus incorporating the possibility raised by Kurland that offspring may be present from the female's previous unions. They conduct a cross-cultural code based statistical analysis of the coincidence of the avunculate with levels of paternity certainty. They even look at societies in which there may be 'some form of culturally sanctioned wife sharing' (Gaulin & Schlegel 1980, 302). On the basis of these tests, they actually find that;

> "[In] low paternal confidence societies there is no tendency for the mother's brother to be important as either caretaker or educator for children of either sex during either early or late childhood." (Gaulin & Schlegel 1980, 304)

They do find some correlation, but without significance (p=0.72 – 0.93). The discrepancy comes not from the lack of societies with low paternal confidence but from the lack of strong avuncularity. They modify the hypothesis to suggest that high confidence leads to high investment in a wife's children, but that low confidence leads a man to channel his investment elsewhere (Gaulin & Schlegel 1980, 304-305). Elsewhere could be maternal kin, non-official suspected offspring (perhaps of another woman) or investment in personal social gain. When looked at in this way they conclude;

> "Our findings are consonant with the idea that cultural patterns leading to heavy male investment in wife's children are common only where mating patterns make it likely that such investment benefits bearers of the male's genes." (Gaulin & Schlegel 1980, 308)

However, they don't suggest any causal direction to the correlation. They are quick to point out that;

> "[F]or any of our findings, the direction of causality could as plausibly go from investment patterns to paternal confidence, in that where a man knows that he will be expected to investing his wife's children, he will make an effort to ensure that they are his own." (Gaulin & Schlegel 1980, 305)

At the same time as Gaulin and Schlegel were conducting their cross-cultural analysis, Flinn (1981) also conducted an empirical study, on the basis that;

> "Alexander's explanation of the mother's brother phenomenon has subsequently been discussed by Greene, Irons and Kurland. However, as yet no comprehensive empirical analysis of Alexander's resolution has been conducted." (Flinn 1981, 444)

Flinn's analysis finds that:

> "Alexander's resolution of the mother's brother phenomenon is consistent with cross-cultural data on both inter and intra-societal variability. However, several aspects of the mother's brother phenomenon remain problematical. First, confidence of paternity is probably not less than ⅓ [his threshold] in some of the societies in which the mother's brother phenomenon is prevalent. Second, conjugal ties in societies with uterine kinship biases are notoriously fragile – among the Nayar "marriage was the slenderest of ties" (Gough 1961a:357), among the Cewa, "marriage ties sit loose" (Richards, 1950:233). The adaptive significance of this correlation has not been examined. Third, the environmental (social and physical) conditions influencing confidence of paternity and hence family structure have not been examined." (Flinn 1981, 446)

To account for the prevalence of the avunculate even where the paternity threshold is exceeded, Flinn suggests that pressure from matrilineal 'kin' could be a factor, and this would be higher where *residence* was matrilocal, since the matrilineal kin group would be more "corporate" (Flinn 1981, 447) under such conditions. Thus Flinn is suggesting that, where matrilineal groups are strong, a man's investment in his own offspring might become secondary, regardless of certainty of paternity (apparently, in fact, regardless of consideration of 'his individual inclusive fitness interests'). Flinn also suggests that the mother's brother phenomenon might exist in patrilineal societies because he could be an independent and disinterested advisor in cases of conflict between paternal kin (Flinn 1981, 450). Flinn's discussion takes in some wider variables which will be looked at further below.

Hartung's 1985 paper is in many ways 'truer' to the 'Alexander/Kurland model' than the intervening treatments. His analysis is centrally focused on the association between certainty of paternity and investment bias favouring matrilineal kin. For Hartung;

> "The hypothesis follows that matrilineal inheritance is a cultural trait that evolved in response to low probability of paternity…" (Hartung 1985, 661)

> "The paternity hypothesis was rescued and made explicit in the context of modern evolutionary theory by Alexander in 1974. Over the next 10 years this provided the impetus leading to numerous theoretical refinements and scholarly and empirical investigations (Flinn 1981; Gaulin & Schlegel 1980; Greene 1978; Hartung 1981b; Kurland 1979)." (Hartung 1985, 663)

Hartung situates the hypothesis of Alexander within a broader trend in the history of anthropology of the 'paternity hypothesis' for matrilineality, which although not theoretically grounded in biology, noted a correlation between matrilineal investment and various conditions contributing to low 'certainty of paternity'. This will be discussed in greater detail below (section 3.2.3). Hartung's innovation is in two areas. First, he suggests that previous models have only considered matrilineal bias as a 'strategy' of males, without considering the 'interest' of females. Further, he suggests that, rather than looking simply at an individual's relatedness to his first generation direct descendents, one should consider that certain forms of 'parental investment' might be passed *down the generations* as inheritance. Thus, he argues, for a given level of 'uncertainty of paternity', as well as a man's relatedness to his first generation putative offspring, relatedness to second generation descendants, third generation and so on all need to come into the calculation. This long-term way of viewing things means that a given level of paternity uncertainty could be argued to be *more* detrimental to the male's inclusive fitness when contrasted with the maternity certainty of matrilineal heirs. On this basis Hartung calculates that the 'paternity threshold' should thus be 0.46 (rather than 0.265). Further, he suggests that the long term interests of females also need to be considered; as grandparents, females should favour investment through daughters whenever certainty of paternity is less than 1.0. Overall, this further elevates the 'paternity threshold' at which all individuals (i.e. the society as a whole) will turn to the "matrilineal solution to uncertainty of paternity", thus avoiding the apparently unrealistically low earlier thresholds.

3.2 PREMISES OF THE DARWINIAN ANTHROPOLOGY TREATMENTS

The last section gave an overview of how the central hypothesis of 'paternity uncertainty' common to all treatments was developed. Some additional assumptions implicit in this hypothesis were noted, and it was suggested that many of these may be somewhat less empirically valid than the Darwinian anthropology treatments required them to be. In the following sections the various premises of this position are further investigated particularly in reference to their implicit interpretation of inclusive fitness theory, as discussed in chapter two.

3.2.1 THE FOCUS ON INDIVIDUALS' STRATEGIES

Alexander's ambivalence about whether to focus on the reproductive success of individuals or genes was a key target (Dawkins 1976, 1989) for Dawkins' later influential reminder (derived from Hamilton) that selection pressure on gene frequencies should be central to evolutionary biology analyses (Dawkins 1976, 1982, 1989, see chapter 2). At certain points of his discussion Alexander appears to grasp that inclusive fitness theory is centrally about selection pressure on genes;

> "Nepotism involves altruism between relatives, the potential for a genetic tendency to spread existing because assisted individuals are likely to be carrying it to the degree that their genotypes are expected to overlap that of the altruist (Hamilton 1964, 1972)." (Alexander 1974, 337)

However, in other sections Alexander clearly follows an individual-level interpretation of the theory. Dawkins' criticism of Alexander picks up on his application of an 'individual' perspective to the dynamics of parent-offspring relationships. There are a few examples of this in Alexander's 1974 paper. In the following passage, for example, Alexander's concluding thoughts highlight the logical intractability of looking at these evolutionary dynamics in terms of individuals;

> "Siblings are often the closest relatives within a population, and they are often one another's closest competitors as well. Thus the extremes of

> cooperation and competition may both be represented in their interactions. It will be useful to know when these interactions evolved because they increased the reproduction of the involved individuals and when they evolved because they increased the reproduction of their parents." (Alexander 1974, 340)

Dawkins quotes from one of Alexander's later passages to illustrate the problem;

> "Suppose that a juvenile mutates in such fashion as to cause an uneven distribution of parental benefits in its own favour, thereby reducing the mother's overall reproduction. A gene which in this fashion improves an individual's fitness when it is a juvenile cannot fail to lower its fitness more when it is an adult, for such mutant genes will be present in an increased proportion of the mutant individual's offspring." (Alexander 1974, 340)

Dawkins suggests that;

> "Alexander's argument… erred through looking at things from the point of view of an *individual*… I believe this kind of error is all too easy to make when we use the technical term 'fitness' [of individuals]. This is why I have avoided using the term in this book. There is really only one entity whose point of view matters in evolution, and that entity is the selfish gene." (Dawkins 1989, 137, emphasis in original)

Alexander's analysis demonstrates how a focus on individual fitness can obscure the underlying process, which can be clarified by reference to inclusive fitness selection pressure on gene frequencies (see chapter 2). Note that it is unclear why Dawkins applied a moral concept to the amoral genetic process (see chapter 1.3.1 for more). Also worth noting is that gene frequency analysis should not prejudice the extent to which selection pressures acting via groups can influence the evolution of a species' behaviours. Recall that Price's (1970) model allows for the analysis of selection pressures operating over multiple scales (see chapter 2.1.7).

It is worth emphasising that, undoubtedly, it is the behaviour of individual organisms (as individuals and in groups) that all students of social behaviour are keen to study and understand. The rationale for the analysis of selection pressure on genes is not to suggest that the behaviour of individuals is not of interest. It is that the evolution of basic behavioural traits is unlikely to be best understood as being a function of "individuals pursuing *their* inclusive fitness". Rather such behaviours may be better understood via the influence of selective processes acting on the frequency of genes (and behavioural traits) via their covariance with reproductive success. This is not simply a brief, unimportant mistake at the theoretical level; Alexander's discussion is dominated by this 'individual-strategy' perspective on genetic relatedness;

> "Indeed, a man's sister's offspring, because of the high confidence of maternity, will be his closest relatives in the next generation whenever confidence of paternity is very low. Thus, if paternity is correctly ascertained only ¼ of the time, then a man's spouse's offspring will average ⅛ like him (and 3 of 4 will be totally unlike him), while his sister's offspring will average 5/32 like him, and all will approach this degree of overlap." (Alexander 1974, 373)

Regardless of the weaknesses of this interpretation of inclusive fitness theory, it was this perspective, and these discussions of *how a male might best maximize his individual inclusive fitness* that were taken away by subsequent Darwinian anthropologists, as suggested at the beginning of the chapter. This is problematic both in the concept of an 'individual strategy' itself, and for the fact that it inevitably has to focus the analysis on the strategies of individual males or females, or both. Most of the Darwinian anthropology treatments focused on the strategy of males, as Hartung (1985) pointed out. This was typical of sociobiological approaches (see Zihlman 1981, see chapter 1.3.2) The following excerpts from the various treatments demonstrate this focus on individual strategies, and the usual focus on males' strategies.

Greene (1978) frames the situation in a way that on the one hand acknowledges that genes are involved, but at the same time seems to suggest that the clearest perspective is to view genes mainly as the vehicles for individual strategies. Such incremental steps effectively submerge selection pressure on genes and allows the focus on circumstances whereby individuals maximise their inclusive fitness;

> "Since natural selection operates through the representation of genes in succeeding generations, one individual can pass on its own genes either by reproducing *or* by helping a relative (with whom some genes are shared by common descent) to reproduce. Thus, if two individuals are sufficiently related, one of them may further its own ultimate reproductive success by helping the other, even at some apparent personal cost." (Greene 1978, 151)

Taking this perspective then leads Greene smoothly into discussions of how a male should further his own ultimate reproductive success under conditions of low certainty of paternity by helping maternal sister's offspring.

Kurland's (1979) analysis suggests that;

> "A group-level analysis is the rule in social anthropology. Evolutionary biology takes the gene as the proper level of functional analysis of behaviour (Dawkins1976)." (Kurland 1979, 157-158)

It is encouraging to see Kurland focus on a gene frequency analysis as fundamental to evolutionary biology theory, though he appears to have misunderstood the inclusive fitness theory position on the significance of demographic groups (see chapter 2.1.6). However, as with others, he soon ignores any further implications of the 'selection pressure on genes' interpretation and the 'interests' of individuals come to dominate the discussion;

> "The optimal female investment strategies may sometimes be at odds with male strategies. And indeed, a woman and her matrilineal relatives may attempt to coerce her husband into acting in ways that increase her inclusive fitness at a cost to his. Disagreements between kin and affine over a male's investment behaviour may lead to conflict over, among other things, inheritance or residence." (Kurland 1979, 166-167)

Kurland also discusses the 'reproductive interests' of the grandparents, and points out that, in viewing their grand-offspring as instances of reproductive success to whom they are equally related, where there is any doubt (at all) over relatedness through males, they would prefer their son to aid a daughter's reproduction of grandchildren for them rather than to attempt to reproduce himself (Kurland 1979, 167-168). We have seen that Hartung expanded on this perspective in his 1985 treatment. Kurland points out that this may be a potential source of conflict since the male himself will only prefer to invest in sister's offspring below the paternity threshold.

Irons makes it clear that his understanding of inclusive fitness theory is that individuals will employ inclusive fitness maximising strategies;

> "This paper has explored reasons for variation in kinship institutions on the assumption that such institutions are generated by the interaction of related individuals pursuing mixed strategies of nepotism and reciprocity." (Irons 1979, 209)

Similarly, here is Flinn's reading of the relevance of Hamilton's contribution;

> "Current biological models of family and kinship behaviour are largely based on Hamilton's (1964) theory of the evolution of social behaviour by kin selection (see also West-Eberhard, 1975). Kin selection theory explains how tendencies to help related individuals survive and reproduce (referred to as "altruism") can be adaptive, that is, favoured by natural selection. Hamilton proposed that it is adaptive for an individual (the "altruist") to assist another individual (the "recipient") when $k>1/r$… Kin selection theory proposes an ultimate reason for behavioural tendencies such as assisting a brother during an axe fight (Chagnon and Bugos, 1979), leaving inheritances to offspring, and other potentially altruistic behaviour." (Flinn 1981, 439-440)

Flinn's reference to Chagnon's work is interesting and this work is discussed briefly in the final section of this chapter. We noted in the last chapter that Hamilton didn't use 'kin selection' until the term (coined by Maynard Smith to highlight problems with the then dominant 'group selection') had become established (see e.g. Hamilton 1975, chapter 2.1.7). Gaulin and Schlegel's (1980) paper continues the basic trend;

> "The essence of sociobiological theory is that individuals act as if attempting to maximize the representation of their genes in future generations." (Gaulin & Schlegel 1980, 301)

However, Gaulin and Schlegel do the reader the service of making the background assumptions underlying the Darwinian anthropology position more explicit, as the next section discusses.

We saw above that Hartung also explicitly relies on an analysis of the strategic interests of male and females acting to maximise their own reproductive success;

> "Inheritance to sister's sons ensures a man's biological relatedness to his heirs, and matrilineal inheritance has been posited as a male accommodation to cuckoldry – a paternity strategy – at least since the 15th century. However, longitudinal analysis of the cumulative effect of female extramarital sex indicates that matrilineal inheritance is most advantageous for women and would more accurately be considered a grandmaternity strategy… [I]t becomes clear that the enhanced association between inherited wealth and a benefactor's genes is much greater for females." (Hartung 1985, 661)

3.2.2 MALE PARENTAL INVESTMENT

Gaulin and Schlegel (1980) give two very useful distillations of the background premises of the Darwinian anthropology position;

> "[Females'] best reproductive strategy is often to provide care to those offspring they do produce. Males, on the other hand, can generally select one of two reproductive strategies or a mix of both. The first is to invest their resources in specific offspring. The second is to mate as widely as possible with little investment in any single offspring, given that at least some of these offspring may survive with maternal investment alone. The former strategy is an effective way to increase male reproductive success only if males aim investment at bearers of their own genes. When genetic relatedness is ambiguous, the latter strategy is often superior." (Gaulin & Schlegel 1980, 301-2)

> "Applying parental investment theory to human society, we can say that a man may emphasise either high investment in offspring or broad procreation, and the distribution of his reproductive effort between these strategies can shift over his life cycle. Given the existence of family and

> kin group, whatever their composition may be, the majority of men in every society invest in children, whether they be a wife's, sister's, lover's, adoptive or some combination… Kurland, following Alexander, has tried to explain some of the cross-cultural variance in male investment strategies. These sociobiologists argue that if the "typical" man, in any society, is clearly the genitor (= biological father) of his wife's children, then these offspring are the most efficient recipients of his investment, in terms of the net effect of the investment on the spread of his genes. If paternity is more ambiguous, then it may be more efficient for him to invest in his sister's children." (Gaulin & Schlegel 1980, 302)

Partly thanks to Gaulin and Schlegel's explicit statement of the hypotheses, we can identify a rough set of premises that accompany these Darwinian anthropology treatments:

1- Notice the understanding of the teleology of the evolutionary process; it is argued that - because acting in some way (investing in his wife's children if paternity is reliable) *would* be more 'efficient' (for individual inclusive fitness maximisation, and to 'spread his genes') – it is predicted that this *should* occur in individual cases.

2- *Parental investment theory* (Trivers 1972), as well as inclusive fitness theory, is employed to suggest that (universally) males always benefit 'their inclusive fitness' by putting effort into investing in their own offspring (but only when they can be certain of paternity). In fact, as Gaulin and Schlegel note, parental investment theory simply predicts a general trade-off between 'parental effort' and 'mating effort', but the latter is in fact scarcely considered by Darwinian anthropology. The familiar teleological error is made with Trivers' theory as with Hamilton's. Being a theory within evolutionary biology, Trivers' insight is fundamentally about the selection pressure acting over evolutionary time, not primarily a description of real-time strategy choice expected to be exhibited by individuals. The first extract above (Gaulin & Schlegel, 301) suggests that individual males' strategies will adjust to certainty of paternity 'in real time', whereas the more influential selective context to consider is the long term ecological and demographic factors typical of the history of the species.

3- Aiding non-descendant genetic relatives is an alternative route to individual inclusive fitness (and female links are 'reliable').

Also;

Because it is clear that, in contemporary human populations, sometimes males do contribute resources towards their wife's offspring, (this being classified as male parental investment) and sometimes they don't, an explanation is required. The Darwinian anthropologists add a final fact to their premises;

4- Some conditions will lead to low "certainty of paternity".

Then the conclusion:

5- A male will invest in his sister's children when certainty of paternity is low.

The avuncular relationship is assumed to result from a male's 'parental investment' instincts – a efficient alternative outlet for his need to express parental investment *when his own certainty of paternity is low*, and a male's best inclusive fitness maximising strategy under these circumstances. Clearly the argument highlights 'certainty of paternity', but is variability of certainty of paternity really at the centre of variations in human social organisation? We have already looked at the use of the concept of goal-directed 'individual strategies'. Is male resource contribution to a female's offspring best understood as being purely as a 'male parental investment' strategy?

Nowhere does the Darwinian anthropology position register what anthropologists had long appreciated as a necessary distinction between *social* fatherhood and *biological* fatherhood (see also Fox (1985), section 3.2.3) and what this might suggest about the 'norms' of the relationship between a male and children. Frazer gave an early example of this distinction;

> "To the Central Australian father (fatherhood) means that a child is the offspring of the woman with whom he has the right to cohabit, whether he has actually had intercourse with her or not. To the European mind, the tie between a father and his child is physical; to the Central Australian, it is social." (Frazer 1910 vol. 1, 336 cited in Schneider 1984, 101)

Schneider recounts that the distinction was later made explicit by Malinowski (1913, 1930);

> "The family, for Malinowski, consists in a woman and the children she bears along with the man with whom the woman and the children are in a more or less stable relationship… So too, the relationship between father and child is based on the relationship between a man and the woman who bears the child, and this socially sanctioned relationship makes him eligible to be the social father." (Schneider 1984, 134)

This suggests that where a significant social relationship exists between a male and children ('biological' offspring or not) it is principally mediated via a stable relationship between the male and the female caring for those children. The avuncular role as a 'social father' is easily understood within this perspective. This perspective is even supported by evidence from Euro-American culture. Lamb (1997) reviews the evidence;

> "Belsky et al. (1984), Lamb and Elster (1985), and Dickie and Matheson (1984) all reported that father's interactions with their infants were influenced by the ongoing quality of interaction with their partners much more profoundly than mother's behaviour was." (Lamb 1997, 119)

Other evidence suggests that, when the male-female relationship is positive and interaction between the pair frequent, males are much more involved with (Belsky et al. 1989), are less aggravated by, and have warmer feelings towards infants (Easterbrooks & Emde 1988). In short, psychological perspectives on parent-child relationships (even drawn from studies of industrial, monogamous societies) suggest that 'genealogical' connection may not be what mediates the social relationship that the Darwinian anthropologists designate as 'male parental investment'.

Even in other areas of research that adopt a biological perspective, using concepts such as the parental effort / mating effort trade-off, male interaction with infants is not necessarily interpreted as 'parental investment'. After extensive field studies, many primatologists prefer to characterise male involvement with a female's infants as 'mating effort'. Stone (1997) summarises the questioning of the 'paternity certainty' hypothesis within biological approaches and notes that alternative interpretations are now increasingly employed;

> "Among multi-male, multi-female species, males participate somewhat in infant care – a finding that some researchers have interpreted not as

> parental investment but as a means of gaining sexual access to the mother (Smuts 1985). Indeed, Smuts and Gubernick (1992) suggest that, among primates generally, male care of infants is better understood as a mating strategy than as a parental investment strategy linked to "paternity certainty." According to this view, a male cares for a female's infants in order to befriend the mother and increase his chances of mating with her. If this hypothesis can be extrapolated to human evolution, male care of infants may have emerged from male-female "friendships" rather than from conditions of greater "paternity certainty." Hewlett (1991) concurs with this view and suggests by extension that, in human evolution, greater male care of offspring came about as a result of stronger social bonds between males and females." (Stone 1997, 31)

More recent biological work on human 'reproductive strategies' also questions many of the Darwinian anthropology assumptions, and suggests that a biological analysis of the 'role' of human males in connection with a female and offspring also should include the influence of mating effort, not only parental effort (Hawkes et al. 1998, 2001; Hrdy 1999, 2000; Marlowe 1999, 2001). Note however that this perspective on males' social investment as mating effort struggles to accommodate the case of avuncular relationships in humans.

Within the Darwinian anthropology treatments, the contradictory stance that a male 'normally' parentally invests in his offspring, yet is proposed not to in the many societies where the avunculate is present, reaches a high point in Kurland's discussion of 'paternity ignorance'. Kurland implies that men who don't 'parentally invest' are essentially 'cheating the system'. The insinuation is that participants 'must really know' about paternity and this leads Kurland to the statement that;

> "Behaviourally, promiscuity belies the articulated ignorance… Of course, for males, paternity ignorance represents a rather impressive "smokescreen" for increased promiscuity. Thus, one male response to the low paternity probability induced by paternity ignorance is simply to increase the number of matings, thereby increasing the number of offspring reared by others." (Kurland 1979, 173-174)

Kurland seems to imply that the 'smokescreen' is deliberate in the pursuit of the 'strategy'; he certainly offers no alternative suggestion as to how this 'strategy' is pursued. Conscious or not, *mating effort* by males is certainly considered a feature of most mammals, but Darwinian anthropologists do not consider this alternative biological perspective in the human case.

Kurland misses a key point; differences between the reproductive behaviour ('strategy') of human males and females both between and within societies *also require analysis*. Even though mating effort and the availability of mating opportunities is usually top of the list when analysing male mammals' reproductive strategies, a possibility such as reduced mating opportunities (coming perhaps from institutionalised monogamy and the formal recognition of paternity) in some societies is not deemed worth investigating. In their commentary on Hartung's paper, Thornhill and Thornhill (1985) illustrate these oversights;

> "The assumption of both Hartung's hypothesis and the hypothesis it proposes to displace is that matrilineal inheritance is an accommodation by males (although for Hartung directed by females) to what they perceive as a bad situation, namely reduced confidence of paternity. This assumption ignores the advantage males gain when freed from allocating large amounts of reproductive effort to securing paternity certainty and to parenting. This freedom allows males to expend more effort in pursuing frequent mating opportunities with multiple females. That matrilineal inheritance accommodates this sort of allocation of mating effort may be perceived by males as a good thing." (Thornhill & Thornhill 1985, 680)

Although the 'mating effort' perspective applied in these contexts also suffers from positing too much real-time strategising to males, (again echoing the concept of 'individual inclusive fitness'), unlike the Darwinian anthropology position, the Thornhills do not assume that male behaviour has evolved to primarily seek to socially invest in 'their' genetic relatives.

3.2.3 THE SEXUAL RELATIONSHIP

We saw in the excerpt from Alexander's paper above (section 3.1.1.), that social patterns such as the avunculate were assumed ultimately to arise or not *"depending on her fidelity"*. That is - it is assumed that 'certainty of paternity' is the central issue; is always to be traced to variability in female sexual behaviour; and is the ultimate cause of lineality patterns. Kurland draws on some anecdotal evidence;

> "Although adultery is exceedingly difficult to quantify, for obvious reasons, ethnographies of matrilineal groups report that the practice is common, frequent, or as it is often coyly put, not infrequent. There is typically, therefore, a great concern with marital fidelity, and jealousy may run high… Many patrilineal societies present a marked contrast – for example, the Nuer (Evans-Pritchard 1940, 1956), the Dinka (Deng 1972), the Tikopia (Firth 1936), the Yanomamo (Chagnon 1968, 1974) and the Akwe-Shavante (Maybury-Lewis 1967). In these, adultery appears to be not only much less tolerated and more severely punished, but also less frequent." (Kurland 1979, 159-160)

To support his position that varying sexual patterns (and the consequent distribution of genetic relatives) are the original source of all attendant social arrangements, Kurland constructs his argument thus: First that sexual exclusivity (the assumed default tendency of humans) may not in fact be the norm in matrilineal societies, and that the uncertainty over paternity that this creates is a 'great concern' (presumably for 'inclusive-fitness-striving' males). Note that fellow Darwinian anthropologist, Hartung, comes to the opposite conclusion about levels of concern over paternity (see below). Second that (the more natural pattern of) sexual exclusivity is maintained in patrilineal societies, and infidelity is strongly punished. But here too, Fox (1993) suggests the opposite reading of, for example, the Nuer position and reminds us of the well supported and long standing (see section 3.2.2) anthropological distinction between 'pater' (social father) and 'genitor' (procreative father);

> "In many patrilineal societies… it is known that the pater is not the genitor… Consider the Nuer for example. Evans-Pritchard (1951) documents quite clearly that intercourse between a woman and a man of her husband's patrilineage is regarded as of no account – a "peccadillo". There are no punishments. As long as the genitor comes from the same patrilineage no harm is done." (Fox 1985, 674)

According to Fox, the supposed correlation between - *levels of paternity certainty* - and - *matrilineal or patrilineal groups* - (the long-standing 'paternity hypothesis' referred to by Hartung) should have been buried long ago;

> "For most anthropologists Sydney Hartland had totally undermined these speculations in *The Legend of Perseus* (Hartland 1894-96), and had given the death blow in the prophetically titled *Primitive Paternity* (Hartland 1909-10). One would have thought that this title alone would have sent the paternity confidence mafia rushing to the dusty shelves, but the work remains unrecognised. Let us consider the final paragraph of *Primitive Paternity* (vol.1, p 325) for its startling contemporary relevance:
> Motherright then is not merely found where paternity is uncertain but also where it is practically certain. Fatherright in the other hand is found not merely where paternity is certain, but also where it is uncertain and even where the legal father is known not to have begotten the children… It follows therefore that the uncertainty of paternity cannot be historically the reason for the reckoning of descent exclusively through the mother." (Fox 1985, 674, quoting Hartland 1909-10, 325)

The Nuer case clearly nullifies Kurland's suggestion about the universal seriousness of sexual infidelity in patrilineal societies. Fox's comments here actually came as commentary on Hartung's 1985 paper. Hartung, like Kurland and Alexander, is unambiguous about the causal relationship between sexual patterns (paternity certainty) and attendant social patterns (lineality). He too relies on the assumption that it is the variant sexual behaviour of females, in departure from more natural patterns, that creates the attendant (and presumably also less natural) phenomenon of matrilineal inheritance;

> "[A]lthough the establishment of matrilineal inheritance may require extremely high levels of female extramarital sex, once established it is likely to be maintained at levels of p [paternity certainty] that reasonably characterise many societies in the ethnographic record… Matrilineal inheritance is a cultural trait that evolved in response to low probability of paternity." (Hartung 1985, 661)

So for Hartung 'female extramarital sex' is the prime cause of all of these derivative patterns as described in classical ethnography. Hartung quotes a number of historic accounts documenting the correlations between matrilineal social organisation and 'female extramarital sex'. In the 15th century, Barbosa comments on the Nayar of south west India;

> "[The women] do not have fixed husbands, and are very free and at liberty in doing what they please… [a man's] children that are born are not held to be his sons… the children are not accountable for more than as children of their mothers." (Barbosa 1866, 105-106, quoted in Hartung 1985)

What is interesting here is that Hartung is quoting a passage that makes his own framing of the situation as 'female extramarital sex' appear to be a misinterpretation of the society's norms (and also casting doubt on Kurland's clams of 'concern with marital fidelity'). Hartung notes De Charlevoix's (1744) documentation of a similar arrangement in North American Huron culture;

> "Hurons may part by mutual consent; this is done without any noise, and the parties thus separated are at liberty to enter into new engagements. These indians cannot so much as conceive how men should make any difficulty about it: 'My wife and I (said one of them to a missionary, who endeavoured to bring him to a sense of the indecency of this sort of separation) cannot live in peace together; my neighbour is in exactly the same sort of situation, we have agreed to exchange wives and are all four perfectly well satisfied: now what can be more reasonable than to render one another mutually happy when it can so easily be brought about, and without hurting anybody?'" (De Charlevoix 1744, Vol. 2; 23, 50, quoted in Hartung 1985)

The norms of male-female sexual exclusivity here are clearly different from those formally recognised in societies where monogamous, sexually exclusive 'marriage' is the norm. The use of the Western symbolic system ('wife', 'marriage', 'extramarital') to describe what are clearly two very *different* sets of cultural norms may be problematic here. For example, in the following encyclopaedic account (again cited in Hartung) giving an explanation of the 'cause' of matrilineal inheritance, the use of the ill-suited English language symbols of 'husband' and 'marriage' is particularly striking;

> "[Women] are allowed by law of the country to marry as many husbands as they please. It is from this custom of women marrying so many husbands, and quitting them again at pleasure, that the children derive their pedigree from their mothers; it being impossible to know their true

> fathers… What is most surprising, and shows the force of custom, this female polygamy is not attended with the least disorder or jealousy; for if one husband sees the arms [armaments] of another at the lady's door, he is satisfied that the place is taken up; and rests contented until he finds the coast clear. It is some consolation, however, to the men, under this female usurpation, that their marriage-engagements are only during pleasure, and that whenever the parties are weary of each other, they part as freely as they meet."[Modern Universal History 1759, Vol.6, 561]

Yet Hartung justifies the perspective (that social patterns are caused by 'female extramarital sex') by the suggestion that these variously described patterns of male-female bonding are best understood as aberrations from a biological norm, which are only sustained by culture;

> "Sexual restriction of females is often put forth as a near universal component of human nature (Daly, Wilson & Weghorst 1982), but, as recognised by the authors of the *Modern Universal History* in 1759, the power of cultural phenomena is suggested by the association between matrilineal inheritance and a relative lack of sexual jealousy…
>
> Wife exchange is a rare but not isolated cultural practice (most common among Eskimos and arctic Indians, see Murdock 1967)." (Hartung 1985, 669)

Where it occurs, lack of sexual jealousy (and 'wife exchange') can only be explained as a cultural deviation from a supposed 'biological norm' of monogamy. The possibility that 'monogamy' (and attendant concepts) are also culturally specific is not considered. In fact, 'wife exchange' (or 'husband exchange') occurs at some level in some 30% of human societies (Hrdy 2000, Broude 1994), and exclusive lifetime monogamy between a male and female characterises very few societies. There are cultures in which an individual enters into multi-male multi-female bonded society marked by ceremonies which strongly challenge the idea of sexual exclusivity as 'normal' (e.g. Hrdy's 1999 summary of initiation rites in the South American Canela). Flinn also lists societies where monogamous 'marriage' is not the norm;

> "Among the Truk, "extramarital affairs are practically universal" (Schneider, 1961:213). Among the Ashanti, "The high incidence of adultery among women is… no new thing, as the elaborate scale of

> adultery damages, which forms part of the traditional legal code, shows" (Fortes, 1950:275). Among the Dobu, "fidelity is very, very rare. Typically his wife will commit adultery with a village 'brother', he with a village 'sister'" (Fortune, 1963:277). Among the Nayar, "It is not certain how many husbands a woman might have at one time; various writers of the fifteenth to eighteenth centuries mentioned between three and twelve" as well as receiving "occasional fleeting visits" (Gough 1961a:358). Thus the adage "no Nayar knows his father" (ibid:364)." (Flinn 1981, 445)

Unsurprisingly, the same adage went for the Canela society discussed by Hrdy. Like Kurland and Hartung, Flinn does not allow all this mounting evidence, that the formal conception of the bond between men and women in such societies might be fundamentally different from that pervasive in monogamous cultures, to question the fundamental premises of the Darwinian anthropology perspective. Flinn is however more cautious in applying other concepts of male-female bonding norms; thus "divorce" receives quotation marks;

> "The high frequency of "divorce" (i.e. dissolution of the conjugal or mating relationship) may in itself result in lowered confidence of paternity, or be the consequence of infidelity." (Flinn 1981, 448)

Although their intention is not to question the assumed biological norms of male-female sexual patterns that their model relies upon, between them these treatments show that such patterns are non-exclusive in many societies. Are non-exclusive sexual relationship patterns best understood as a culturally imposed (Hartung 1985) aberration from *a more natural pattern of sexual exclusivity*? The assumption is that Euro-American society follows the 'most natural pattern' - that monogamy and a preoccupation with sexual exclusivity might themselves be cultural aberrations is never considered.

If one focuses on sexual behaviour *per se* as the primary cause of all subsequent social patterns, further analysis of the circumstances that might also shape patterns of sexual behaviour are obscured. Circumstances surrounding the different bonding norms of males and females in different societies are nowhere addressed by Hartung, Kurland or Alexander. Rather, lineality patterns and all related social features are assumed to arise from the proposed independent variable – sexual behaviour.

3.2.4 ASSUMPTIONS ABOUT PRIME CAUSES OF LINEAL SOCIAL SYSTEMS

Kurland finishes his paper with a claim of an open-minded position regarding the causality involved;

> "The paternity threshold model predicts how idealised human actors ought to respond to given levels of paternity certainty. However, this model may give the impression that low paternity probability "causes," for example, the avunculate. Not only is this an absurd use of mechanical causation, but it is equally reasonable to conclude that the avunculate "causes" low paternity probability. These aspects of human sociality and biology do seem to correlate, but clearly this association must be mediated by a host of biological, demographic, economic, and psychological variables that are at present rather imperfectly understood." (Kurland 1979, 175)

Notice that the "ought" of the first sentence gives a clear impression of the goal-directed interpretation of inclusive fitness theory used by Darwinian anthropologists. The final sentence is a statement of the official Darwinian anthropology agnosticism regarding mediating 'proximate mechanisms' which will be reviewed more thoroughly in the next section, and is relevant to the approach taken in the current research. Despite these words of caution about the causality involved, Kurland relies on assumptions of default arrangements for human social group organisation;

> "Thus where promiscuity is more prevalent, more tolerated or more easily achieved… there will be lower levels of paternity certainty. There will be a concomitant emphasis on the avunculate and other matrilateral relationships as evidenced by investment patterns, residence, and other forms of social behaviour." (Kurland 1979, 157)

> "The present model lends some support to Murdock's (1949) contention that matrilocal-matrilineal societies easily revert to patrilocal-patrilineal societies. The paternity threshold (=0.265) is low, and thus may be easily realized. This low paternity threshold easily leads to the emergence of patrilineal, patrilateral, or patrilocal patterns that are, in fact found in many matrilineal groups. Once the paternity threshold has been passed, only a radical alteration in residence, male mobility, promiscuity or female choice will bring the average paternity probability again below a fourth.

> Thus it is not too surprising that only 15 per cent of societies in Murdock's (1957) sample are matrilineal." (Kurland 1979, 176)

Despite Kurland's claims of open-mindedness, the default position is assumed to be one of patrilineal society (notice "revert"). The default mating set-up is assumed to be one where males and females are formally bonded and a male's connection to his offspring is *highly certain* (centrally important because of the assumption of male parental investment). It is therefore concluded that matrilineal systems are necessarily characterized by low-certainty of paternity because this is the primary cause of matrilineal organization, and because such organization is only sustained whilst the factors creating this low paternity certainty remain in place. Thus, ultimately, a male's certainty of paternity (via 'female promiscuity') is assumed to dominate all other variables of social organisation. Kurland makes explicit the assumptions of the approach, without investigating those assumptions.

We have seen Hartung's ideas about the centrality of 'female extramarital sex' causing matrilineal inheritance. He also has ideas about the link between matrilineal inheritance and lineality patterns in general;

> "Given anthropology's traditional emphasis on lineality, inheritance to sister's sons has been seen as a consequence of reckoning one's lineage through female ancestors. The opposite could be the case; i.e. matrilineality may be a consequence of inheritance to sister's sons, and changes in lineality systems may generally follow changes in inheritance patterns." (Hartung 1985, 669)

In marked contrast to Hartung and Kurland's exclusive focus on 'female promiscuity', Irons, refreshingly, does not put this as prime cause. Instead, he suggests that analysis of patterns human social behaviour should take into account a number of variables;

> "[T]he variation in the specific activities which individuals are able to carry out in a particular environment to increase their own and their allies' reproductive success, and the magnitude of the effect of these activities on reproductive success. Environmental constraints and opportunities define an optimal pattern of investment and this, in turn, defines an optimal pattern of residence, rules for inheritance of property, the nature

> of marriage contracts, and other social patterns governing relationships among primary allies." (Irons 1979, 208)

Irons defines 'environment' as "everything external to an individual which affects his or her inclusive fitness. Other individuals and their expected modes of behaviour are often the most salient feature of the environment when it is defined in this way." (Irons 1979, 184). Irons also notes unusual social patterns in societies characterised by unusual resource conditions, and brings in consideration of what anthropologists would identify as *local* or perhaps even *cultural* factors influencing the behaviour of males (and females);

> "In contrast to female behaviour, male behaviour is more variable from one society to another. This reflects a greater variation for males than for females in the optimal pattern of investment among mating effort, parental effort and other kin effort… [I]n industrial societies male and female investment patterns have come to resemble one another. Both sexes are characterised by low fertility, high parental investment in a few offspring, and little kin effort other than parental effort." (Irons 1979, 205)

In an interesting reversal of perspective on the necessity of bonding between males and females, Irons goes on to suggest that the variables may in fact be related in the following manner;

> "It might seem at first glance that women would always be interested in securing males investment for their children and that a husband who is convinced he is related to her children by ½ would always be a more reliable investor than a brother who can be related by no more than ¼. However, this would not be the case if a cooperative group of related females is more effective at rearing children than a husband-and-wife pair or a polygynous group consisting of one husband and several unrelated females. This is apparently the situation faced by Tiwi women [a society Irons discusses in the paper]. Given this condition, women may not be willing to do anything for a husband which disrupts the effectiveness of a cooperative group of related females. This could easily mean a woman would be unwilling to move at marriage or to tolerate a husband who interferes in the relations between herself and her co-resident female kin. This condition may underlie uxorilocality and frequent divorce in many societies. If the value for child rearing of a related group of females is very

> high and the value of male assistance in child rearing very low, women may be reluctant to move at marriage, disinclined to value marriage once conflict emerges between a husband and wife, and set little store in fidelity as a means of giving a man paternity confidence." (Irons 1979, 210-211)

Here Irons places resources available to females (and thus female residence patterns) centrally, male-female bonding and other demographic patterns peripherally.

We saw that Flinn attaches some relevance to the fact that matrilineal groups are more 'corporate', and thus influential when residence is matrilocal, although he had a slightly different view of how this might fit into the larger picture. In fact, Flinn mainly follows the Kurland/Hartung emphasis for the causal chain leading to lineality patterns. Nonetheless, in discussing the correlates of matrilineal inheritance systems, Flinn documents a number of the variables whose casual relationship fits Irons' scheme, especially the possibility that females may not place a high value on being tied to one male;

> "[T]here are some societies in which confidence of paternity appears to be greater than the 1/3 threshold, but the frequency of divorce is high (i.e. typically an individual will have been divorced three, four or more times in a lifetime). In such societies, the parental role of the father is usually reduced compared to the parental role of the father in societies with low rates of divorce. This is especially true if the offspring remain with the mother after separation." (Flinn 1981, 448)

Here, Flinn has come across a correlation that cannot easily be explained by the 'Alexander resolution'; if males are confident of paternity and have a universal tendency to invest in their own offspring, why should they not do so? Flinn himself has some ideas about causality, although the first is essentially the Alexander hypothesis;

> "Biological theory suggests the following reasons: First, altruism dispensed by a man to his offspring might be utilised by his offspring's uterine half-siblings who are unrelated to him… (see also Kurland 1979). The second reason… is the potential impediment to parental behaviour caused by the separate residence of father and offspring. If the distance between residences is such that the cost of parental behaviour is greatly

> increased or makes appropriate parental behaviour difficult… then coresiding sister's children may become more advantageous recipients of a male's altruism." (Flinn 1981, 448-449)

In these two excerpts, Flinn has noticed certain conditions surrounding the tendency of males to discontinue "investment in offspring". Flinn suggests that the physical distance between the male and the offspring may exert too high a cost *even for a male who is certain the offspring are his.* Such occurrences are difficult to account for under a 'Male Parental Investment Strategy' model. The perspective which emphasises the importance of the male's ties with the mother of the children (e.g. the anthropological 'pater', and see above 3.2.2) can easily accommodate such evidence.

3.3 THE MOVE TOWARDS ANTHROPOLOGICAL HYPOTHESES OF 'DESCENT'

Although some of the Darwinian anthropology treatments have mentioned the relationship between residence patterns and lineality patterns, this relationship and the factors influencing it are secondary to the 'certainty of paternity' factor in their causal models. The prominence of descent conceptions of kinship was in fact in decline within anthropology by this time (see chapters 8 and 9). Nevertheless the association between residence and/or subsistence options and kinship had long been part of anthropological analyses of social patterns. In this section we find that some of the Darwinian anthropology treatments mention these analyses (whilst still emphasising 'investment strategies'), and by 1985 (in commentary on Hartung) many were suggesting that it might be worth paying more attention to these perspectives.

Taking a leaf out of Irons' book, Flinn (1981) goes on to note ecological and subsistence resource influences on variation in the pattern of social relationships;

> "Morgan (1870) Tylor (1889), Spencer (1967), Lowie (1920), among others championed the relative role of men and women in subsistence as relevant to family structure and kinship organisation. When women are the primary providers, they suggested, residence is likely to be matrilocal

> and kinship matrilineal… [As] a woman's economic and social position relative to her mate's increases, the importance of her mate's economic and social contribution to her offspring may decrease… As the ability of males to reciprocate in the conjugal relationship diminishes, family structure is likely to become increasingly "matrilfocal" (and usually but not necessarily uterine kin biased – see Gonzales, 1970). When males have little contribution to make to the family, women may gain from a short-term, multiple-mate strategy (Gonzales 1969; Stack, 1975)." (Flinn 1981, 450-452)

Later, under a section titled 'Residence: An Adaptive Choice?' Flinn considers this association further;

> "Linton... states that "matrilineal descent is normally linked with matrilocal residence, patrilineal with patrilocal"… This hypothesis, in terms of a biological theory, suggests a functional association between the flow of altruism, residence, and kinship behaviour. If the biological basis for this hypothesis is valid, then the potential altruism an individual is likely to receive in a given location should be a criterion for residence choice. If a male child receives the most altruism from his mother's brother, avunculocal residence is expected if co-residence enhances the benefits derived. If the flow of altruism changes over an individual's life-history, then different residences at different life history stages are predicted… Predictably, socio-economic status affects residence choice, as "men of wealth and distinction are able to reverse the usual rules of residence" (Richards, 1950:248) keeping their wives and putative offspring – of whose paternity they are likely to be relatively certain – resident with them. In general, patterns of residence appear to be associated with the flow of altruism, although the direction of causality is difficult to determine." (Flinn 1981, 453-454)

As Irons suggested, there is an alternative perspective: Where females can be self-sufficient in an environment, and local warfare is not present to elevate the value of males, daughters might simply remain in their natal group (matrilocal residence) and need not attach themselves to a husband, since they can get assistance from other local females. In turn, males do not need to commit themselves to one female, and overall, 'paternity confidence' is not emphasised. This perspective, outlined by Irons (above), mirrors a well established anthropological position that had, by this time, been clearly set out by cross-cultural anthropologists working on the ontogeny of descent groups (more below), perhaps most notably by Ember and Ember (1971, 1975, see Pasternak et al. 1997 for a review).

Gaulin and Schlegel also noted the influence of residence and are generally careful about specifying causality;

> "The most significant distribution that we find is between paternal confidence and residence, where high paternal confidence appears with father-centred residence… whereas mother-centred or mother's-brother-centred residence is more likely in low paternal confidence societies. Thus fathers are more likely to exert authority in households where they are more likely to be the genitors of the wife's children, and less likely to do so where they are not. An alternative explanation is that where males exert authority over the households in which their children live, they are more able to make certain of their paternity of these children than men who do not have the same degree of household authority." (Gaulin & Schlegel 1980, 304-305)

By the time of his commentary on Hartung's 1985 paper, Kurland had become much more interested in possible ecological factors contributing to 'certainty of paternity';

> "[W]hat is cause and what is effect in the association between the avunculate and paternity?… What kind of ecologies foster low or variable paternal probabilities? By specifying some of the ecological factors associated with matriliny or low paternal probability, we might begin to flesh out the proximate costs and benefits associated with alternative marital and inheritance strategies, and thus begin to understand the ultimate benefits and costs associated with the concomitant reproductive and nepotistic strategies." (Kurland 1985, 675-676)

Reunited in the same commentary, Flinn was by now also keen to suggest that subsistence factors needed to be investigated;

> "The environmental determinants of probability of paternity and inheritance strategies are an important area for further analysis. This is where evolutionary and ecological hypotheses may have the most to offer students of human social behaviour. Murdock (1949), Aberle (1961), Gough (1961), Hiatt (1980), and other anthropologists have hypothesised that subsistence strategies may affect patterns of kinship and inheritance.

> Their arguments are compatible in many respects with models from behavioural ecology (e.g. Krebs and Davies 1978). Humans exhibit a wide range of mating and inheritance patterns, providing a useful empirical base for comparative analysis of evolutionary and ecological hypotheses… Studies of cultural change in matrilineal societies (e.g. Fuller 1976; Gough 1961) also indicate that change is initiated by individuals pursuing mating and kinship strategies that are influenced by economic concerns… The corporate nature of kin groups tends to break down with modernisation and the accompanying individual ownership of property (Fuller 1976; Gough 1961)." (Flinn 1985, 673-674)

But this perspective is little different from the established anthropological perspective mentioned above (although the latter doesn't elevate the centrality of 'mating and kinship strategies' or 'certainty of paternity'). In fact, in the same commentary, Lancaster gives an overview of just such an account of the typical ecological/subsistence correlates of lineal groups, starting with matrilineality;

> "Women contributed very substantially to the food supply. The scale of village life was small. Women could be star players in the socio-political arena while raising large families and tending the family gardens… But in areas where better soils and climates gave rise to denser populations and civilisations supported by intensified peasant exploitation of a restricted land base, human organisation developed a different set of adaptive rules. The need to fight for scarce land, the need to add male to female labour in a more productive type of agriculture, and increased socio-political scale all combined to elevate the importance of male over female roles... Now the problem with Hartung's argument is that he erroneously uses strategies (wealth inheritance, control of female sexuality) and concepts (cuckoldry) associated with the peasant adaptation to interpret patterns (such as matriliny) associated with the [non-peasant] tribal world. Contrary to Hartung's view, extramarital sex as only been highly restricted for women in the peasant and post-peasant worlds. Only in those worlds has there been a marked tendency, and need, for men to transfer wealth to their sons." (Lancaster 1985, 676-677)

Lancaster thus gives an overview of the anthropological position given more extensive treatment by Ember and Ember (1971, 1975 and others). Hartung describes Lancaster's commentary as "an authoritative sounding panoramic view of prehistory is given in the "you are there" style."

(Hartung 1985, 686). However, a number of these suggestions are resonant with the ideas aired by Irons and later by Flinn (1985 above) as well as the large number of anthropologists noted by them.

Nevertheless, as discussed in chapter one, a more fundamental problem with the lineage perspective had been identified by anthropologists; the whole way in which social organisation was understood in anthropology was being revised by accounts such as Schneider's (1984). In particular, the long-standing assumption that kinship is predicated (directly or indirectly) on genealogy was itself being questioned.

In a sense then, Darwinian anthropologists were in search of a phenomena that required their perspective. Not only was the Darwinian anthropology emphasis on the genetic relatedness at the heart of 'kinship' totally out of tune with anthropology's contemporary critiques of the connection between genealogy and 'kinship'; the associations between residence, subsistence and male-female bonding patterns were well modelled by traditional anthropological approaches and required few of Darwinian anthropology's concepts. Were connections with biology to be made, it seemed that behavioural ecology (largely independent of inclusive fitness theory, reviewed in chapter 5.3) might be more compatible with an analysis of residence and lineality patterns than the Darwinian anthropology models.

3.4 PROXIMATE MECHANISMS

Alexander's original paper did not discuss the psychological or behavioural mechanisms whereby, as he saw it, individuals end up accurately tracking their optimal 'individual inclusive fitness' maximising strategies. In fact this agnostic position has characterised early sociobiological positions in general, not merely Darwinian anthropology treatments of the avunculate and matrilineality patterns. So important has this discrepancy been that another school making reference to evolutionary biology has grown up in the space left over – evolutionary psychology. Their critique of Darwinian anthropology on this basis will be sampled briefly below. First however, the avoidance of discussion of proximate mechanisms in the treatments we have come across so far is illustrated.

Kurland makes a number of introductory comments explaining the focus of his treatment;

> "It is not the purpose of this paper to trace the phylogeny of the avunculate from some reconstructed ancestral nonhuman primate society… [I]n this paper, I attempt to explicate this aspect of human kinship and social organisation in terms of basic evolutionary biological principles. Such a functional explanation of the avunculate can indicate only why such behaviour is biologically adaptive, that is, specify its *ultimate* causes in the process of natural selection. Functional explanations of behaviour rest on such evolutionary arguments. This does not imply that the many previous explanations about the *proximate* psychological or economic causes of human kinship behaviour are incorrect or irrelevant… Evolutionary biologists who study the evolution of sociality are concerned with the prediction or explanation of how behaviour maps onto the environment, *not* how genes map into behaviour. For an evolutionary biologist who investigates social behaviour, the particularly salient environmental stimuli relevant to explanations of an actor's behaviour are those very stimuli generated by the ongoing behaviour of other actors in the population… Postulating the existence of a gene that obliquely codes for "altruism" is only a simplifying and heuristic procedure… such modelling procedures in no way commit one to strict genetic determinism or reactionary politics." (Kurland 1979, 146-147, emphasis in original)

The latter guarded comments are best understood in light of the reception of Wilson's controversial position on genes and behaviour (see below). However, Kurland's claim that biologists are concerned with "how behaviour maps onto the environment, not how genes map onto behaviour" too often results in a complete absence of any investigation of evolved proximate behavioural or psychological mechanisms of social behaviour. Irons (1979) follows the basic line of argument that individual behavioural choices are expected to maximise the individual's inclusive fitness, regardless of mechanisms;

> "It should further be noted that such choices are not consciously made in terms of inclusive fitness. Exactly what sort of thought processes do lead to actual decisions is a complex issue not dealt with in this paper. Here it is merely assumed that whatever these thought processes are they tend to produce the same result that a conscious weighing of choices would have

> in terms of their effects on inclusive fitness… [T]he objective is to demonstrate how one can derive specific testable hypotheses from the general proposition that interaction among primary social allies is governed by investment choices aimed at maximising inclusive fitness." (Irons 1979, 182-4)

Flinn concludes his treatment by outlining the Darwinian anthropology methodology, highlighting the assumption of individuals' inclusive fitness maximising goals;

> "The biological model of family structure and mating-marriage systems presented here does not rely on genetic differences to account for behavioural differences. Rather, the variability of a few basic factors – confidence of paternity, genetic relatedness, and the distribution of reproductive resources in the physical and social environment – are postulated to explain behavioural differences within the context of individual adaptation… Modern evolutionary theory posits that individuals strive not only to survive, but also to reproduce and increase the survival and reproduction of genetic relatives." (Flinn 1981, 465)

Gaulin and Schlegel include a brief statement on the relevance of proximate mechanisms in their final discussion:

> "The more proximate (e.g. psychological) aspects of how such changes [in investment norms] might be mediated fall outside of the realm of the present study but one might hypothesise a sort of cognitive consistency mechanism." (Gaulin & Schlegel 1980, 307)

Hartung is even less interested in proximate mechanisms, but does make a statement on genetic influences;

> "The association between inheritance practice and probability of paternity illustrates an important relationship between culture and biology. Sociobiology need not argue that differences between societies result from differences in genes for inheritance strategy. The argument here is only that the association between traits can be predicted by evolutionary theory." (Hartung 1985, 669)

By the time of his (1985) commentary in Hartung, Kurland had become more interested in discussing mechanisms;

> "What is the psychological reality of the paternity hypothesis? I think less stringent or improbable mechanisms are required than does Barkow (1984). Indeed, I do not believe it would be too difficult to find evidence of a human ability to track paternity; mice and monkeys seem capable of it (see papers in Hausfater & Hrdy 1984). For example, the cross-cultural data on sexual jealousy provide prima-facie evidence for a male-specific psychology predicated on paternity uncertainty (Daly, Wilson & Weghorst 1982; Symons 1979). But perhaps Hartung and I have not thought through the exact causal, ecological, or psychological mechanism implied by the paternity hypothesis." (Kurland 1985, 676)

3.5 CRITICISM FROM OUTSIDE DARWINIAN ANTHROPOLOGY: EVOLUTIONARY PSYCHOLOGY

From the above excerpts raising questions about mechanisms, it is notable that many of the treatments simultaneously emphasise that cultural differences need not be caused by genetic differences. Are the two points - a keenness to emphasise a lack of genetic "determinism" and the avoidance of focus on proximate mechanisms – related in any way? Although Alexander did not discuss these issues in his 1974 paper, he did in his 1979 book;

> "If there is one thing that natural selection has given to every species, it is the ability to adjust in different fashions to different developmental environments. That is what phenotypes are all about, and all organisms have phenotypes. If there is an organism most elaborately endowed with flexibility in the face of environmental variation, it is the human organism." (Alexander 1979, 95)

Like the others, Alexander suggests that attempts to draw conclusions about genetic limitations are "a profound misunderstanding of biology and evolution" (Alexander 1979, 95). For this reason, human behaviour is to be explained by revealing how, in different environments, people modify their attitudes and practices so as to maximise their individual inclusive fitness.

This position of the Darwinian anthropologists is undoubtedly motivated by a desire to avoid the controversy generated in the wake of publication of

Wilson's 1975 book *Sociobiology*, and a distancing from some of Wilson's premises, especially his position on the relative place of phenotypic flexibility or genetic differences. Wilson, in turn, was of course reacting against what he saw to be the errors of the 'environmentalist position';

> "Dobzhansky (1963) stated this position as follows: "Culture is not inherited through genes, it is acquired by learning from other human beings… In a sense, human genes have surrendered their primacy in human evolution to an entirely new, nonbiological or superorganic agent, culture. However, it should not be forgotten that this agent is entirely dependent on the human genotype." Although the genes have given away most of their sovereignty, they maintain a certain amount of influence in at least the behavioural qualities that underlie variations between cultures… Variations in the rules among human cultures, however slight, might provide clues to underlying genetic differences, particularly when it is correlated with variation in behavioural traits known to be heritable." (Wilson 1975, 550)

Although many social scientists and biologists alike would broadly agree with Dobzhansky's position (see chapter 1), Wilson's position is quite different. Wilson is clearly quite wrong that variations between cultures require the positing of genetic differences. His unsupported claim that cultural differences reflect genetic differences runs contrary to the foundation that Boas and others had provided for the contemporary social sciences (see chapter 1), and was perhaps the main reason why Wilson's thesis attracted strong opposition. Alexander, seeking to avoid controversy, refers to behavioural plasticity and conversely avoids discussion of proximate mechanisms involving underlying genetic influence, and the possibility of uncovering Wilson's 'differences'.

Unfortunately, the Darwinian anthropology caution and official agnosticism on proximate mechanisms, whilst being a 'safe' position, itself is unsustainable, and eventually gave rise to a further counter position – that of the evolutionary psychologists (see Symons below). We saw above that Darwinian anthropologists advanced the hypothesis that individuals simply strive to maximise their individual inclusive fitness. Kitcher (1985) discusses this hypothesis;

> "Let us suppose that Alexander, Kurland, and others succeed in showing that in certain environments particular forms of social behaviour maximise the inclusive fitness of those who engage in them. What exactly have we learned about human nature? The careful qualifications issued by Kurland and Alexander seem to block the most direct connection between premises about inclusive fitness and conclusions about fundamental features of human social behaviour. So it seemed to three reviewers of Alexander's book. In the postscript he reports that these readers "were disappointed that I had not more explicitly attacked the problem of what constitutes human nature, identifying its limits and explaining the consequences" (Alexander 1979, 279)." (Kitcher 1985, 282-283)

Later in his book, Kitcher suggests that;

> "A commonsense picture of human motivation that I shall call folk psychology… supposes that people typically act so as to maximise the chances of obtaining the things that they perceive as valuable… [W]hen it is put to work in the social sciences, folk psychology offers an account of the proximate mechanisms that underlie human actions… we can envisage the possibility that evolutionary biology might enrich folk psychology by charting the evolutionary history that underlies the proximate mechanisms folk psychologists invoke. Here we discover one way in which Alexander's [behavioural plasticity] version of sociobiology might be articulated… Clear-headed folk psychologists ought to recognise that there are evolutionary explanations for whatever mechanisms underlie our familiar human aspirations… let us call this discipline *evolutionary folk psychology*… I conclude that if evolutionary folk psychology is a correct program for the understanding of human social arrangements, then the [Darwinian anthropology] claims about maximisation of inclusive fitness under special social arrangements do not contribute the evolutionary explanations that are really needed." (Kitcher 1985, 285-288)

Kitcher's point about the wrong-headedness of Darwinian anthropology's agnosticism about proximate mechanisms was well argued, and these mechanisms (particularly the psychological mechanisms) are what the current research investigates. A similar line of argument was taken up later by Symons (see below). The only alternative stance that Darwinian anthropology could take was to;

> "[S]uppose there is some general mechanism for calculating the expected payoffs of the available courses of action and to maintain that this always comes into play in the causation of our social behaviour… the general fitness calculator, quietly grinding out what is in our best evolutionary interests." (Kitcher 1985, 289)

Positing such a general purpose 'inclusive fitness calculator' makes references to potentially complex proximate mechanisms unnecessary. In the Darwinian anthropology assumption that individuals do act to maximise their inclusive fitness in some automatic way, such a general mechanism is implicitly invoked. But we saw in chapter two that this is an erroneous interpretation of inclusive fitness theory. Fox makes a similar point to that of Kitcher about a folk psychology view of motivation;

> "Are they really motivated to "maximise their inclusive fitness," as the sociobiological formula has it?… Is it not enough to say that we have a number of simple and observable motives, and if we act on these… if we get all of these right, then "maximisation of inclusive fitness" will follow. We do not have to posit hidden and unconscious motives that go directly to maximisation choices (Fox 1986)." (Fox 1993, 225)

Symons, in his influential paper "A Critique of Darwinian Anthropology" (1989) made a number of critiques of this neglect of the features of evolved behaviours (DA below = Darwinian anthropology);

> "DA's central hypothesis is that "evolved behavioural tendencies" cause human "behaviour to assume the form that maximises inclusive fitness" (Irons 1979b, 33). Turke and Betzig (1985) state this hypothesis as a formal prediction: "Modern Darwinian theory predicts that human behaviour will be adaptive, that is, designed to promote maximum reproductive success through available descendant and nondescendant relatives." (p 79)… [T]he key terms in [this] quotation are used in DA to bypass the question of phenotypic design in characterisations of adaptation." (Symons 1989, 131-132)

> "As Tooby and Cosmides [1989] note, "expectations of adaptation predict behaviour only approximately, and do not appear to lead further than the characterisation of modern behaviour as either adaptive or maladaptive, that is, as consistent with expectations derived from fitness maximisation models or inconsistent with them. On the other hand, knowledge of the

> innate psychological mechanisms that actually produce behaviour should predict behaviour far more closely.'"" (Symons 1989, 141)

It was on the basis of the potential value of investigating proximate mechanisms that evolutionary psychology emerged. This school has largely stayed away from applications to human kinship patterns, with the exception of Daly and Wilson (see also chapter 1.6). In an explicit application to 'kinship' Daly and Wilson, surprisingly, voice their *support* for the position advanced by the Darwinian anthropologists;

> "Following a suggestion by Alexander (1974), evolution-minded anthropologists have discussed the incidence of extrapair paternity that would be necessary for putative fathers to actually be more closely related, on average, to their sister's sons than to their wives' sons (Kurland 1979). Avuncular inheritance is indeed cross-culturally associated with conditions conductive to low levels of paternity confidence (Flinn, 1981; Gaulin & Schlegel, 1980), and if those levels are seldom or never quite low enough to make the sisters' sons closer kinsmen than wives' sons, we should remember that these inheritance decisions are not the man's alone and that his parents can always be surer of their relationship to his sister's children than to his own children (Flinn, 1981; Hartung, 1985)." (Daly et al. 1997, 274)

Daly and Wilson go on to question the accuracy of Sahlins' (1976) summary that human 'kinship' patterns are potentially independent of consanguinity. In doing so they thus challenge Schneider's position, as well as most of the ethnographic evidence (see chapter 1), and ignore the findings of other sociobiologists (e.g. Silk 1987, see chapter 1.2). In this respect, despite the stated adherence to a focus on proximate mechanisms, these evolutionary psychologists' privileging of genetic relatedness is actually stronger than that of earlier sociobiologists. They claim that amongst many other 'universal' features of human kinship systems;

> "Kinship relations are universally understood to be arrayed along a dimension of closeness… [which] is always negatively correlated with the characteristic number of genealogical links defining them, and hence positively correlated with genetic relatedness (r). The first five universals are apparently conceded by even the most biophobic of commentators. Where cultural determinists have tried to draw the line is on this sixth

> point. In a famous attempt to refute the applicability of Hamiltonian theory to human affairs, Sahlins (1976) claimed to have demonstrated "that the categories of 'near' and 'distant' vary independently of consanguinal distance and that these categories organize actual social practice" (p.112). He had, of course, demonstrated nothing of the sort. His evidence consisted entirely of typological descriptions of alleged practices in certain societies which, if verified, would indicate only that the correlation between "closeness" and genetic relatedness is sometimes less than perfect… the categories of "near" and "distant" do not "vary independently of consanguinal distance," not in any society on earth." (Daly et al. 1997, 281-282)

It is particularly ironic that Daly and Wilson's actual lack of understanding of anthropological thinking is such that they even go on to implicate *Schneider himself* as being in support of their position that genealogy (by which they read genetic relatedness) is really what, for all societies, 'kinship' is all about;

> "In our society and many others, the interests of the firstborn young may be especially well served by familial solidarity, and it is of interest that firstborns are disproportionally inclined to assume the role of family genealogist (Salmon, 1997). Ours is certainly not what anthropologists would call a kin-based society… Both sexes are interested in genealogy as a hobby, but several studies suggest that women are particularly inclined to maintain active kin networks (Hogan & Eggebeen, 1995; Schneider & Cottrell, 1975). Troll (1987) provides evidence that men's kinship bonds operate through the influence of their wives or parents, and that older women typically adopt the role of "kinkeeper," providing family news updates, organizing get-togethers, maintaining contacts among family members, and training daughters or granddaughters for the role. And North American women do indeed know their own genealogies better than men (Salmon & Daly, 1996; Schneider & Cottrell, 1975)." (Daly et al. 1997, 284)

Of course, Schneider's point was precisely that this cultural valuation of 'kinship' (genealogy) may be particularly elaborated in Euro-American cultures (Schneider 1984, 201). His point arguably receives further support here from Daly et al.

3.6 MORE ATTENTION TO PROXIMATE MECHANISMS?

As is clear from the analysis so far, the assumption that individuals always act in accordance with the interests of their own 'inclusive fitness maximisation' characterises Darwinian anthropology as a whole. Kitcher gives an example of a case where the Darwinian anthropologists' own data might better be interpreted with an appeal to proximate mechanisms that respond to circumstantial cues. He discusses Chagnon and Bugos' (1979) suggestion that genealogical relatedness mapping onto individual allegiance patterns should be clearly visible in a confrontational situation where such alliances are crucial. They illustrate this with the example of a Yanomamo 'axe-fight' (they use the blunt ends) that occurs between two acquaintances during a period of 'village fissioning'. Chagnon and Bugos claim that;

> "[T]he major variable appears to be closeness of genetic relatedness: individuals seemed primarily to "decide" to aid others on the basis of the degree of relatedness obtaining between themselves and other participants in the fight. (Chagnon & Bugos 1979, 222)." (Kitcher 1985, 312)

But Kitcher deliberately adopts a 'proximate mechanism' perspective;

> "Perhaps people fight on the side of those they like and against those they dislike, or those they like less. Given a propensity to like close kin, especially those with whom one has been reared, and also to be well disposed towards those with whom one has a history of reciprocal exchanges, it may be that the resultant behaviour will coincide with the action recommended by inclusive-fitness maximisation. However, there is no unconscious computation of coefficients of relatedness… This suggestion nearly makes sense of the data. Almost all Mohesiwa's supporters are close relatives – siblings, uncles, close cousins – or people who come from the new village. In three cases visitors from the new village who are more closely related to Uuwa than to Mohesiwa fight with Mohesiwa, presumably on the grounds of solidarity against the hosts [village]." (Kitcher 1985, 312-313)

Notice that the proximate mechanisms that Kitcher suggests are of the same kind invoked by Hamilton and Dawkins (see chapter 2). He suggests that simple 'rule of thumb' mechanisms (e.g. liking those you have been reared with) might by-and-large have met the inclusive fitness criterion (in typical evolutionary environments). Kitcher further discusses some of the coefficients of relatedness which characterise the variously allied individuals in the Yanomamo confrontation, including this interesting fact that a small number of individuals actually go to the aid of the key combatant to whom they are *less* closely related (though the genealogical relationships are fairly distant). Kitcher continues;

> "A *preliminary* explanation of the patterns of alliance is that people choose to defend close kin… and choose sides on the basis of village loyalty where factors of kinship do not proscribe a course of action… My tentative suggestions only show that folk psychology, with its strategy of appealing to proximate mechanisms promises to provide a far more illuminating account of the alliances in the fight..." (Kitcher 1985, 315)

Kitcher's suggestion is then that, in place of invocation of a 'general purpose inclusive fitness maximising mechanism', an investigation of evolved proximate behavioural mechanisms should inform biological analyses of social behaviour. Can we add this suggestion about proximate mechanisms to the discussion about the potential role of 'situational cues' (e.g. Dawkins 1979, reviewed in chapter 2.2.1)? The area of theory concerned with how social behaviours are mediated is investigated in the next chapter.

CHAPTER FOUR – 'KIN RECOGNITION' THEORY: CONTEXT DRIVEN OR POSITIVE POWERS?

4.1 INTRODUCTION

In reviewing basic inclusive fitness theory in chapter two, I argued that social behaviour tendencies will evolve to reflect the typical genetic relatedness of the (social) situations that individuals encounter, and that those behavioural tendencies are expressed within. An understanding of how this might occur is crucial. It was suggested that this could in principle happen via circumstantial rules of thumb (as in Dawkins' 'in the nest' example), or perhaps via 'positive discrimination' (Hamilton 1987) of *actual genetic relatedness*. These alternatives clearly have a bearing on how biological theory should be interpreted. Does it predict that individuals have evolved social behavioural dispositions *to cooperate with actual* genetic relatives? Or simply that the expression of social behaviours will be cued in those situations and contexts in which genetic relatives would typically (in past evolutionary environments) have been encountered?

At the close of chapter three we found that Kitcher (1985) made a suggestion to illustrate that evolved 'proximate' psychological mechanisms may be involved in the expression of social behaviours in humans. In its basic components, his suggestion was that; being reared with a person may lead to 'liking' the person and; 'liking' a person may lead to helping them. Clearly Kitcher supplied no great detail with this suggestion, and no evidence to support its validity as an accurate interpretation of how inclusive fitness theory applies to humans (his intention was simply to illustrate the conceptual point). Nevertheless, Kitcher's suggestion is not very different from Dawkins' suggestion, and even the discussion by Hamilton (1964) about the development of social behaviours in birds according to context and situational cues (see 2.2.4). In Kitcher's example the situation or context is 'reared with' (although this lacks any clear definition) which leads to 'liking' (a form of social bonding) and this in turn is the 'proximate mechanism' that mediates the social behaviour.

In the following three chapters, we investigate the question of 'actual genetic relatedness' in the mediation of social behaviours more closely. Does the notion that human social actions may be mediated by situational cues and social bonds stand up against comparative evidence from other mammals and primates (chapters 5 and 6)?

Before we turn to this evidence, it would be useful to know how biologists usually conceptualise the possibilities. In this chapter (following on from the brief introduction in chapter 2), the theoretical alternatives are more thoroughly reviewed. The question of *how* social behaviours might 'track relatedness' – whether this is 'context driven' or by 'positive powers' of discrimination (Hamilton 1987) – has become known as 'kin recognition theory'. The term 'kin recognition' is to 'kin selection' as 'statistically tracking replica genes' is to 'inclusive fitness theory'. Kin recognition is the accepted language of the field which studies the extent to which organisms' behaviour effectively discriminates 'relatedness'. Although, as noted in chapter two, the term 'kin' is inappropriate in applications to human social behaviour, the terminological use in this chapter nevertheless follows the convention in this field.

4.2 TRACKING GENETIC RELATEDNESS – BASIC CONCEPTUAL POINTS

As I set out in chapter two, inclusive fitness theory should not be interpreted to mean that organisms are selected to evolve social behaviours *per se* regardless of the environmental and ecological selection pressures upon doing so (see Sherman 1980, section 2.1.6). Similarly, mechanisms for accurately identifying genetic relatives are obviously not necessarily expected to evolve as ends in themselves. If a context of interaction between individuals who may be genetic relatives does not occur with any consistency over the evolutionary history of a species, there will be no positive selection upon behaviours which are sensitive to that relatedness (or lack of relatedness).

Although experiments to demonstrate a *lack of* an evolved ability to distinguish genetic relatives are understandably rare, a few tests of kin recognition ability in some species illustrate this; for example, in work on the salamander *Hemidactylium scutatum* researchers summarized their findings thus;

> "Larvae of Hemidactylium did not show statistically significant kin recognition ability or the ability to recognize conspecifics based on familiarity. These results are consistent with the larval ecology of these organisms, which is characterized by a low population density and no schooling behavior." (Carreno et al. 1996, 293)

Similarly, in the northwestern salamander *Ambystoma gracile*, upon finding no ability to distinguish conspecifics on the basis of either familiarity or genetic relatedness, researchers concluded "scrutiny of the life history and ecology of this species may provide important clues as to the selective forces operating on the evolution of kin discrimination in larval amphibians." (Walls et al. 1996, 965)

Other research has produced evidence that individuals of a variety of species (both vertebrate and invertebrate) may, in laboratory conditions, cannibalise siblings and/or offspring; Amazonian poison frog *Dendrobates ventrimaculatus* (Summers & Symula 2001); Indian meal moth *Plodia interpunctella* (Boots 2000); ponerine ant *Gnamptogenys striatula* (Blatrix & Jaisson 2002); red-spotted newt *Notophthalmus viridescens* (Gabor 1996); ladybird beetle *Harmonia axyridis* (Osawa 1992); marbled salamander *Ambystoma opacum* (Walls & Blaustein 1995). The occurrence of such behaviour strongly reinforces the point that inclusive fitness theory should not be understood to simply predict that individuals will inevitably recognise and engage in positive social behaviours with genetic relatives. Consideration of the demographics of the typical evolutionary environment of any species is crucial to understanding the evolution of social behaviours. As Hamilton (1987) puts it, "Altruistic or selfish acts are only possible when a suitable social object is available. In this sense behaviours are conditional from the start." (Hamilton 1987, 420).

To reinforce the importance of considering the conditionality of the evolution of social behaviours on demographic context, even where an ability to effectively recognise and behaviourally discriminate does exist, this may be very specific to typically encountered contexts. For example, Sherman et al. (1997) suggest that certain classes of genetic relatives will inevitably fail to be recognised where no precedent for encountering such genetic relatives has existed in past evolutionary environments, and conversely, non-relatives may be treated in the same way as relatives, if they are encountered in circumstances typically constituted by relatives;

> "[C]ircumstances favouring recognition may be rare, or may have been rare until recently. Female Belding's ground squirrels behave nepotistically only to daughters and sisters. More distant relatives (granddaughters, second cousins) are treated like non-kin (Sherman, 1980). These distant kin are infrequently alive simultaneously (Sherman, 1981b). Either selection has not favoured abilities to learn templates to recognise distant relatives (perception component), or the rate of interaction with them is so low that the optimal acceptance threshold is restrictive, excluding distant kin (action component). As another example, bird species that have long been exposed to brood-parasitic cowbirds or cuckoos consistently reject parasite eggs, whereas species whose nesting habitats have been recently invaded (e.g. due to forest fragmentation) tend to accept all eggs in their nest, including those of parasites…" (Sherman et al. 1997, 92-93)

The evolutionarily typical context of interaction is thus what constitutes the selection pressure upon inclusive fitness effects, and 'kin-directed' behavioural discriminations. Consistent with the discussion of interpretation of inclusive fitness theory in chapter two (see section 2.1.7), Sherman et al. also make the general point that selection pressure acts on long-term, reliable statistical associations, rather than the specific relatedness coefficients that constitute any given encounter;

> "Recognition-promoting alleles spread because of indirect statistical associations between the recognition cue (i.e. the location) and the presence of the recognition promoting allele in conspecifics. When frequencies of interactions with relatives at a particular location (e.g. a nest burrow) are sufficiently high, selection may favour universal acceptance at that location… In species exhibiting location-specific behaviour, parents do occasionally rear non-kin due to mix ups (in bank swallows: Hoogland and Sherman, 1976; Belding's ground Squirrels: Sherman 1980; paper wasps: Gamboa et al., 1986b), but these recognition errors are rare. Moreover, as we have seen, recognition systems based on phenotypic cues of genetic or environmental origin are not immune to errors either." (Sherman et al. 1997, 94)

In short, just as demographic constraints should be understood to apply to the potential evolution of social behaviours (chapter 2.1.6), so too, demographic patterns will influence what mechanisms of 'kin discrimination' might evolve. These must thus be considered in any application of biological theory to the behaviours of a particular species.

4.3 WHAT IS KIN 'RECOGNITION'?

Although there are good reasons for 'kin recognition' to evolve apart from for social discriminations (see section 4.5 below), the growth of interest in 'kin recognition' was in large part directly stimulated by Hamilton's work on inclusive fitness theory, reviewed in chapter two. All those engaged in the debate about 'kin recognition' (e.g. Alexander 1979, Dawkins 1982, Blaustein 1983, Waldman 1988, Grafen 1990, Sherman et al. 1997, Tang-Martinez 2001) and its relationship to inclusive fitness theory are essentially agreed about the significance of the latter as a selection pressure on social behaviours.

But, as suggested, a complicating factor is that, apart from specifically social acts, there are other behaviours (such as inbreeding avoidance) that may benefit from a sensitivity to genetic relatedness. Because of this, evidence of a kin recognition ability is not in itself evidence that social behaviours are also present, and even less that their expression is contingent on such recognition.

The distinction between an ability to distinguish genetic relatedness and the behavioural acts that may or may not accompany this ability underlies the difference between '*kin recognition*' and '*kin discrimination*' in the established terminology (see e.g. Waldman 1988, Holmes 1990, Hepper 1990), and will be employed in the following analysis. Kin *discrimination* can be said to occur when an individual exhibits differential behaviour towards genetic relatives, but may effectively come about in typical ecological and demographic conditions without the need for 'sampling' of genetic relationship i.e. '*recognition*' *per se* (see the example of eusocial aphids, below). Conversely, even if individuals have an ability to differentiate between others *on the basis of actual genetic relatedness*, i.e. *recognition* is possible (as demonstrated perhaps under laboratory conditions), it is not necessarily always accompanied by any behavioural discrimination, let alone discrimination involving significant levels of social behaviour.

Given the need for subtlety in this area, some theorists feel that 'kin recognition theory' has been beset by conceptual confusions (e.g. Grafen 1990, 1991, Tang-Martinez 2001);

> "Ever since Hamilton (1964) proposed his revolutionary concept of kin selection to explain social evolution and the evolution of "altruistic" behaviours, there has been a strong interest in kin recognition and the mechanisms by which animals are able to distinguish between their kin (genetically related individuals) and non-kin (genetically unrelated individuals). Kin recognition is considered such an important process for the operation of kin selection, that many behavioural ecologists seem to implicitly assume that specialised mechanisms allowing individuals to distinguish their kin from non-kin must have evolved." (Tang-Martinez 2001, 21)

I suggest that this same unsafe assumption also characterises simplistic applications of inclusive fitness theory to human social behaviour. Let us look at an example of this distinction between kin *discrimination* and kin *recognition*. An investigation of kin discrimination in the eusocial aphid *Pseudoregma bambucicola* found that unrelated alien workers placed into a novel colony were never attacked or removed by soldiers, and conversely soldiers placed into an alien colony provided altruistic defence even within that 'non-kin' context (Shibao 1999). In this case, no *kin recognition* could be said to occur, even though the species is highly social and the typical behaviour of individuals in a typical context of the colony amounts very effectively to *kin discrimination*. In fact only aliens of distantly related species were attacked by soldiers (congeneric species such as *P. koshunensis* were ignored). These results agree with those of other social aphids (Shibao 1999), and to the extent that any 'recognition' mechanism at all is present, it would more accurately be described as a form of 'species recognition'. In demonstrating the distinction between *discrimination* and *recognition* this example emphasises the need to consider the demographics that have shaped the social behaviour typical of the species.

An important immediate conclusion from such investigations is that, in any particular instance, the *expression* of social behaviours – social behaviours that may have been shaped by selection pressure on inclusive fitness – need not be limited to a situation which is *actually* comprised of genetic relatives. This is the case even if the *evolution* of those behaviours can be said to have come about via their meeting the inclusive fitness criterion in *typical past environments*. This contrast between the *evolution* of a behaviour and its actual *expression* is a crucial conceptual point. It is particularly relevant to understanding how inclusive fitness theory applied to humans can be consistent and compatible with findings in anthropology (chapters 1 and 8).

Given that *typical* context can clearly play an important role in channelling social behaviours towards genetic relatives (kin discrimination), as mentioned above, many have suggested making a distinction between two classes of 'recognition'; on the one hand what might be called 'inactive context driven' recognition and on the other, 'positive powers' of recognition (Hamilton 1987). The former might also be called 'locational' (Holmes and Sherman, 1982) or 'indirect', and the latter 'direct' cues (e.g. Waldman 1988). (An overview of these mechanisms is provided below).

These subtleties demonstrate that caution is necessary over how to interpret what is meant by 'kin recognition', and its distinction from 'kin discrimination'. Because behaviours that amount to 'discrimination' can potentially be achieved without any need for 'recognition' yet reliably allow the discrimination of behaviour towards genetic relatives, Grafen (like Tang-Martinez above) has questioned the very notion of '*kin* recognition' as a unitary phenomenon;

> "'Do animals really recognise kin in a way that is different from the way they recognise mates, neighbours, and other organisms and objects?'. Certainly animals use recognition systems to recognise their offspring, their siblings and their parents. But to the extent that they do so in the same way that they recognise their mates and their neighbours, I feel it is unhelpful to say they have a kin recognition system." (Grafen 1991, 1095)

Grafen goes on to suggest that the term *'kin recognition'* might be reserved for those cases where organisms are demonstrated to use 'positive powers', particularly genetically labelled cues, to track genetic relatedness, of which he finds precious little experimental evidence (Grafen 1990). Tang-Martinez (2001) advises similar caution on invoking 'recognition';

> "[T]he fact that animals benefit from engaging in spatially mediated behaviors is not evidence that these animals can recognise their kin, nor does it support the conclusion that spatially-based differential behaviors represent a kin recognition mechanism (see also discussions by Blaustein, 1983; Waldman, 1987; Halpin 1991). In other words, from an evolutionary perspective it may well be advantageous for kin to aggregate and for individuals to behave preferentially towards nearby kin, whether or not this behaviour is the result of kin recognition *per se*." (Tang-Martinez 2001, 25)

Having set out the conceptual pitfalls, it is necessary to look in more detail at the range of potential recognition or discrimination mechanisms, particularly with a view to understanding the distinction between what Hamilton (above) called 'inactive context driven' recognition and 'positive powers' of recognition.

4.4 OVERVIEW OF POSSIBLE MECHANISMS

There are generally understood to be a few possible 'mechanisms' whereby 'kin recognition' could be said to occur (whatever the type and level of any accompanying social discrimination). It should be clear that some of these are 'positive powers' and others 'context driven'. Blaustein (1983) gives a useful summary;

> "There are four possible mechanisms proposed for kin recognition (reviewed by Alexander 1979; Bekoff 1983; Dawkins1982; Holmes and Sherman 1982).
>
> 1. *Recognition can be based on spatial distribution.* - If relatives are distributed predictably in space, altruistic acts might be selected for if the acts are directed preferentially towards those individuals in a particular location. Such a location may be a home site or territory.
>
> 2. *Recognition can be based on familiarity and prior association.* - If relatives predictably occur in appropriate social circumstances, recognition could occur through social learning (Alexander 1979). Thus, individuals of the same litter within the same nest or those from one clutch may learn to

> recognise "familiar" individuals (see Bekoff 1981, 1983 for a detailed discussion of familiarity and recognition). Relatives might also recognise one another if they predictably meet in the presence of a third individual who is familiar to each of them. One example of this may be two maternally related half-siblings from different litters that interact with their common mother (Holmes and Sherman 1982).
>
> 3. *Recognition could occur through phenotypic matching.* - In phenotypic matching, an individual learns and recalls the phenotypes of relatives or of itself (assuming phenotypic similarity is correlated with genetic similarity). The individual then assesses similarities and differences between its own phenotype and unfamiliar conspecifics. Thus, for example, if chemicals or odors are involved in kin recognition, they may have a genetic component, but must be learned for kin recognition to occur.
>
> 4. *Recognition could be achieved by the action of recognition alleles.* - Phenotypes could be used in recognition independent of learning if recognition alleles existed. In this system, the phenotypic marker (e.g., a particular chemical or odor) and the knowledge of that marker have genetic bases." (Blaustein 1983, 749)

Blaustein observes the distinction between 'context-driven' and 'positive' recognition by going on to note that in mechanisms (1) and (2) above "kin *per se* are not actually recognised" (Blaustein 1983, 749).

Mechanism (2), recognition based on familiarity and prior association, whilst not necessarily being recognition of kin *per se* nevertheless warrants the name 'recognition' if some kind of learning (and subsequent remembering or equivalent process) does occur. Recognition via a mutually familiar 'third individual' (see Blaustein above) or 'go-between' has also been called 'mediated recognition' (Holmes & Sherman 1983), and will be seen (esp. chapter 5) to be important for certain forms of recognition of genetic relatives outside the direct mother-offspring relationship, as Blaustein suggests.

Mechanism (3), phenotype matching, has broadly two possibilities; learning a template phenotype from relatives, or learning one's own phenotype. The former must be "learned during interactions in unambiguous social circumstances" (Lacy & Sherman 1983, 490) i.e. requires that the initial context of learning is reliably constituted by actual genetic relatives, thus effectively joins mechanisms (1) and (2) as relying on 'context-driven' recognition since 'kin *per se* are not actually recognised' independently of the initial context of template formation. Indeed, external-referent phenotype matching can be thought of as similar to the above 'recognition via a third individual' (or location), but based on a learned template of certain features of that common referent, rather than in its direct presence. For this reason some have named this type of recognition 'indirect familiarity' (e.g. Porter 1988). A similar point is made by Halpin;

> "[I]t could be argued that recognition by familiarisation and recognition by phenotype matching are nothing more than different forms of the same 'association' or 'familiarisation' mechanism (see also Halpin & Hoffman 1987; Porter 1988). Furthermore, recognition by association and by phenotype matching do not differ in the origin of the cues upon which they rely. In both cases the cues may be of either genotypic or environmental origin." (Halpin 1991, 250-251)

Self-referent phenotype matching (the second possibility for mechanism (3)) is a potentially more direct 'positive power' of discrimination, and has more in common with mechanism (4), recognition alleles, albeit with some important distinctions between the two. In fact it is precisely these latter two possibilities that are referred to by Hamilton (1987) as 'positive powers' of recognition and the similarities and differences between them will be considered below (section 4.6).

4.5 OTHER SELECTION PRESSURES ON RECOGNITION

It is important to note that evidence of a species' ability to recognise genetic relatives as distinct from non-relatives is not evidence that such recognition functions to mediate social behaviours *per se*. The ability to recognise and potentially discriminate may instead mediate other types of behaviour. This is particularly relevant for a consideration of selection pressure upon the more 'direct' or 'positive' forms of kin recognition.

In particular, an ability to distinguish genetic relatedness may be selected via benefits from *inbreeding avoidance* behaviour. Recognition for purposes of inbreeding avoidance can be considered as one component of 'mate recognition', along with species recognition, and recognition of sex

(Sherman et al. 1997). Selection pressure upon recognition mediating these various forms of discrimination (in the sense of discrimination outlined above, section 4.3) thus means that evidence for the presence of a recognition ability in any given species *per se* is not necessarily evidence for 'kin discrimination' (engaging in significant social behaviours with genetic relatives). Hamilton makes a similar point;

> "It does not follow… that ability to discriminate degrees of relatedness automatically implies that kin selection is the model relevant to its origin. In fact, since even earlier than Darwin, it had been realised that most organisms tend to avoid closely inbred matings. The reasons must have to do with the function of sexuality and this is not quite yet resolved (see e.g. Bell, 1982; Shields, 1982; Hamilton, 1982); but whatever the function is, here must be another set of reasons for discriminating. Some animals clearly do use discrimination for purposes of mate selection. Japanese quail for example evidently use an early imprinting of their chick companions towards obtaining, much later, preferred degrees of consanguinity in their mates (Bateson 1983)." (Hamilton 1987, 419)

4.6 'POSITIVE POWERS' OF RECOGNITION

Whilst the same four possible types of mechanism as proposed above (section 4.4) could equally evolve to promote recognition for inbreeding avoidance, or for species recognition (e.g. Grafen 1990, Sherman et al. 1997), an extension of this point needs consideration: There are certain behaviours (such as social behaviours) which, if contingent upon particular types of 'positive powers' of recognition of genetic identity, would in principle be subject to positive selection upon genetic suppression ('modification'), whilst other behaviours (such as inbreeding avoidance) contingent on the exact same recognition mechanisms would not. The notion that the expression of certain of genes' effects might be subject to selection pressure upon modification by other genes was discussed in chapter two (2.2.5); we consider this assessment of which effects might realistically evolve further here.

Self-referent phenotype matching has also been dubbed 'the armpit effect' (Dawkins 1982). There is an important distinction between this mechanism, which works via perceptually learned phenotypic similarity, and the recognition gene (or 'green-beard') effect, although the two might appear superficially similar (see also discussion in Dawkins 1982, 143-155) and both are both classified as 'positive powers' of discrimination by Hamilton (1987).

Unlike the 'green beard' effect, the hypothesised self-referent phenotype matching mechanism is proposed *not to rely* on a label expressed by a single gene (or set of closely linked genes) to assess genetic similarity. Instead, the attribute(s) used as the 'template' for comparison to other individuals are potentially genetically unlinked from the gene promoting the proposed effect, and additionally the phenotypic attributes that serve as the reference template to be learned may be numerous and widely distributed across the genome (Lacy and Sherman 1983, Hamilton 1987). I cite here from Dawkins (1982) who gave the first clear illustration of the proposed mechanism and its distinction from the 'green-beard effect' (see chapter 2.2.5 for more on the latter);

> "The only way for the green-beard effect to arise is by incidental pleiotropy. A mutation must arise which just happens to have two complimentary effects: the label or 'green beard', and the tendency to behave altruistically towards labelled individuals. I have always thought such a fortuitous conjunction of pleiotropic effects too good to be true. Hamilton also noted the ideas' inherent implausibility, but he went on '…exactly the same *a priori* objections might be made to the evolution of assortative mating which manifestly has evolved, probably many times independently and despite its obscure advantages' (Hamilton 1964, p. 25)… Why is it that the green-beard effect seems so much more far-fetched than assortative mating? It is not just that assortative mating is positively known to occur. I suggest another reason. This is that when we think of assortative mating we implicitly assume *self-inspection* as a means of facilitating the effect. If [blue] individuals prefer to mate with [blue] individuals, and white with white, we do not find this hard to believe because we tacitly assume that individuals perceive their *own* colour. Each individual, whatever his colour, is assumed to be obeying the *same* rule: inspect yourself (or members of your own family) and choose a mate of the same colour. This principle does not stretch our credulity by demanding that two specific effects – colour and behavioural preference – are controlled pleiotropically by the same gene. If there is a general advantage to mating with similar partners, natural selection will favour the

> self-inspection rule regardless of the exact nature of the recognition character used…
>
> [The] 'armpit effect' is here being used as a general name for any case of an animal inspecting himself, or a known close relative, and discriminating in favour of other individuals with a similar smell or with some other perceived similarity. The essential difference between the green-beard effect and the armpit effect is as follows. The armpit self-inspection behavioural rule will lead to the detection of other individuals that are similar in some respect, perhaps in many respects, but it will not specifically lead to the detection of individuals that possess copies of the gene mediating the behavioural rule itself… the green-beard effect is quite different. Here the important thing is that a gene (or close linkage group) programs the recognition specifically of copies of *itself*. The green beard effect is not a mechanism for the recognition of kin. Rather, kin recognition and 'green-beard' recognition are alternative ways in which genes could behave as if discriminating in favour of copies of themselves… A 'kin-selection gene' is, in a sense, working for itself alone, but it benefits the other genes in its genome as well. There will therefore not be selection for modifiers that suppress it. Armpit self-inspection genes would be a special case of kin-recognition genes, and are likewise not outlaws." (Dawkins 1982, 145)

In principle a 'self-referent phenotype matching' system which is based on learning of a template from the individual itself (what Dawkins calls the armpit effect) might be influenced by some (multi-locus) genetic endogenous labels. Such a multiply-influenced phenotype should in principle reliably correlate with ancestral relatedness (not just genetic identity at a single locus). The proposed multi-locus basis also requires a stable polymorphism of multiple rare alleles in order to ensure that identity at various loci does indeed correlate with genetic relatedness across the whole genome (the genetic constitution that common ancestry reliably provides).

Dawkins' useful summary remains an accurate description of the status of 'positive powers' of discrimination within biological theory. Note that even here, the 'armpit effect' requires learning, even if from 'self' in the absence of other individuals (although how often 'self' would be the only reference available in non-laboratory conditions is subject to debate, see below). Of course, Dawkins' account in itself provides no information about the 'real world' situation; whether such 'positive powers', or alternatively, context-dependent discriminations are observed in species under study. The following chapters will look at the evidence.

It is worth noting a further theoretical subtlety associated with the 'green-beard' effect. Hamilton draws an important distinction between the kinds of *discrimination* which could be associated with the 'learned' versus such 'innate,' green-beard types of recognition;

> "The [self-referent phenotype matching] system outlined above was based on a minimal kind of 'social learning' (Alexander 1979). Prior to application in behaviour, the learning, which in this elemental case was self-habituation, can be done by the individual in total isolation. Could there be any mechanism of kin recognition that does not need learning of any kind? In fact, there do seem to be effects describable as kin recognition which are like this, but at the same time there are also *reasons to believe that they cannot evolve into nepotistic patterns of any complexity*." (Hamilton 1987, 23, emphasis added)

Hamilton goes on to give the example of 'the case of the trees' cited in chapter two (see chapter 2.2.5). Recall that we saw in chapter two that social cooperation may be subject to modification if mediated by 'recognition genes' and consisting of interactions which every other locus in the genome is not 'in agreement' about regarding the inclusive fitness criterion, because, e.g. non-relatives are being actively prioritised. However, behavioural discriminations on such a 'minority basis' would in principle *not be* subject to modification if they imposed no comparative cost (and perhaps some benefit) on the rest of the genome. Discriminatory behaviours involved with inbreeding avoidance would potentially meet this requirement. Thus Hamilton goes on to give an example where features of a learned template based on phenotype (but in fact influenced by a small number of genes) appears to mediate such a discrimination;

> "The house mice which show mating preferences based on unlikeness of certain genes in the histocompatibility complex (Boyse, Beauchamp and Yamazaki, 1983). This effect is very surprising, perhaps the more so when it is known that it is mediated through odour coming from urine. We cannot do more than note here what appears to provide the basis for a minimally learned discrimination system of the kind already outlined, and

> that it seems to have potential to become 'green-beardy' [involving recognition genes] in so far as the effect is concentrated in the small *H-2* region of the chromosome. But once again, we do not expect anything describable as an innate kin recognition adaptation, used for social behaviour other than mating, for the reasons already given in the hypothetical case of the trees." (Hamilton 1987, 425)

In fact there is evidence that in the natural state of interaction between individuals, the 'template' for the inbreeding avoidance system in this species is usually learned from others and is not 'self-referent' (see next chapter). Nevertheless Hamilton's point is that the criterion of 'no-relative-cost' to the rest of the genome could be fulfilled in the case where inbreeding avoidance results from a small number of genes involved in detection of genetic relatedness. Even in cases where genetic identity at one point of the genome does not in fact correlate with genetic relatedness across the whole genome (as it typically would in the case of ancestral relatedness), avoiding mating in such a hypothetical case may not constitute a significant enough cost (relative to the benefit other loci receive when ancestral relatedness is present) to select for modification of the effect. But for 'social behaviour other than mating', discrimination on this basis is not expected.

The implication of Hamilton's point it that, even in a case where 'innate' forms of recognition appear to be present, theory predicts that *social* behaviours will not be mediated on this basis. Other theorists agree with Hamilton on this. Emphasising that the 'template' to be used as a referent for measuring relatedness in self-referent phenotype matching must rely on a learned sampling, rather than innate, Sherman et al. note that;

> "There are no clear examples of genetically encoded kin-recognition templates (Alexander 1990; Pfennig & Sherman 1995). This is probably because, as a result of meiotic shuffling of genetic cues and spatiotemporal variation in environmental cues, the characteristics of desirable recipients (kin) will differ for different actors, rendering genetically encoded templates unreliable. In addition, intragenomic conflict should thwart expression of selfish 'recognition alleles' (template loci linked to both recognition cue and decision rule loci: see Alexander & Borgia 1978; Alexander 1979; Ridley & Grafen 1981)." (Sherman et al. 1997, 81)

In short, for discriminations that constitute ‘social behaviour other than mating’, innate recognition is not expected; and Sherman et al. (above quote) confirm that (even for mating discrimination) there are no clear examples of innate templates.

Self-referent phenotype matching would be advantageous for inbreeding avoidance, and perhaps for certain other social discriminations where context driven cues are not available (see also Hamilton 1987). However, for species in which individuals are typically born into a minimal social environment in which other individuals are present, ‘other-referent’ template formation may take precedence over ‘self-referent’.

Thus some cautions are necessary when interpreting possible evidence of self-referent phenotype matching which may be produced under non-typical laboratory conditions. Some have suggested that evidence of self-referent phenotype matching may, in many cases be a product of experimental artificialities of individuals being reared in isolation from conspecifics, and forming a phenotype based ‘kin-recognition’ template on the basis of the only phenotype they experience – their own. In short, experiments demonstrating the operation of self-referent phenotype matching in the lab do not necessarily reveal the comparative influence of such mechanisms on ‘kin recognition’ in natural conditions (see for example Grafen 1990, Alexander 1991, Blaustein et al. 1991, Gamboa et a 1991). Sherman et al. give the following caution;

> “Assessing the relative importance of different kinds of cues in kin recognition can be difficult because, as Breed (1983) and Carlin (1989) noted, whenever experimental subjects are reared in uniform environments, where the only detectable differences are in gene products, investigators may erroneously conclude that they use only genetic labels to recognise kin. The issue that must be addressed is whether such cues would be supplemented, or even supplanted, in nature by variable environmental cues.” (Sherman et al. 1997, 77)

Holmes (1990) also urges caution in analysing experimental results, and emphasises the importance of consideration of the typical ecology of the species under study;

> "The point is that to interpret laboratory-derived discrimination abilities in an adaptive framework, one must be knowledgeable about the behaviour and ecology of the organism in its natural environment. Indeed this knowledge is critical in designing an ecologically relevant laboratory study in the first place." (Holmes 1990, 453)

Holmes now brings us to a consideration of the fundamental place that ecology and patterns of interaction in natural environments play in the mediation of kin discriminatory behaviours. To conclude this section, the key point is that consideration of typical context is necessary even when appearances suggest that the most extreme form of 'positive powers' of discrimination (self-referent phenotype matching) may be present.

4.7 INTRODUCTION TO CONTEXT-DRIVEN 'RECOGNITION'

In this section we introduce consideration of what Hamilton called "context driven" recognition. As in the point made by Holmes (the above quote), I want to suggest that an understanding of a species' typical ecology can immediately give insights into the typical regularity and reliability of the contexts of interaction of genetic relatives. The following chapter (chapter 5) will look in greater detail at the importance of considering a species' typical context and review evidence for context-driven recognition.

That kin discrimination can effectively occur in eusocial aphids (section 4.3) without any positive powers of recognition is unsurprising when considering the normal ecology of the species. Similarly, results on Belding's ground squirrels make sense when considering the typical context of interaction of genetic relatives;

> "Cross-fostering studies in the field (Holmes & Sherman, 1982) and laboratory (Holmes, 1984, 1986a, 1994) indicate that nestmate females learn each other's odours just before weaning (when litters normally begin to mix), and later treat each other as siblings, regardless of their actual relatedness. Social learning of these kin-recognition templates does not increase acceptance errors in nature because unrelated pups rarely cohabit the same nest burrow (Sherman, 1980)." (Sherman et al. 1997, 82)

In general, the variety of opportunities for context driven recognition is best illustrated by consideration of key, reliable ecological features of the focal species. Waldman agrees;

> "Knowledge of the mechanisms by which kin discrimination occurs, the extent to which different classes of relatives can be recognized, the cues upon which recognition is assessed, and the means by which social preferences develop is important for assessing how closely behavioral tactics of individuals conform to those predicted by kinship-based models. Studies of kin recognition are most valuable, however, when framed within ecologically appropriate settings, and analyses of the contexts in which kin discrimination occurs can clarify how recognition mechanisms function." (Waldman 1988, 543-544)

The study of any potential mechanisms of context-driven social behaviour cannot be conducted in abstraction from consideration of basic features of the species' evolutionarily typical living environment. This varies for each species, and is not directly observable. How context-driven social behaviours can be analysed is discussed in the next chapter (chapter 5), and evidence for presence of such context-driven mechanisms in mammal species is also reviewed.

4.8 SUMMARY

Chapter two reviewed the biological theory surrounding the *evolution* of social behaviours. This chapter has introduced some concepts surrounding the part played by the (evolutionary) criterion of *genetic identity* in the actual *expression* of social behaviours, which is typically treated (somewhat inappropriately) as 'kin recognition theory'. Between these two chapters, we can begin to grasp both the scope and the limits to which genetic relatedness can be said to be connected with social behaviours.

Environmental and ecological factors, amongst others, will determine a species' demographic possibilities. Inclusive fitness theory specifies one necessary condition (a criterion) upon the evolution of social traits of positive covariance with reproductive success, which will become relevant *if* a significant and durable context for the interaction of replica genes is provided by the environment (and suitable mutations are present). If they do meet the inclusive fitness criterion, replica genes (and social traits) may do so partly as a result of ancestral relatedness (e.g. via interactions between genetic relatives). For a social trait then, we can say that correlations involving genetic relatedness may have been an important factor in its frequency increase and thus *its evolution* within a population (or species). But this does not translate into genetic relatedness being a necessary factor in the *expression* of a social trait. As Sherman clearly demonstrates (see above and chapter 2.1.6), when we consider the proximate *expression* of social behaviours; genetic relatedness cannot be assumed to be a *sufficient* condition for their expression (e.g. the salamanders) and nor can it be assumed to be a *necessary* condition for their expression (e.g. the aphids).

As first suggested in chapter two (2.1.6), a consideration of typical situations of interaction is crucial to understanding the evolution and modes of expression of social behaviours. Section 4.6 demonstrated that, even in cases where 'positive powers of discrimination' (such as self-referent phenotype matching) seem to occur in laboratory conditions, the species' typical contexts of interaction cannot be ignored.

Moreover, 'context-driven' mediation of social behaviour is widely accepted as a strong theoretical possibility by inclusive fitness theorists and 'kin recognition' theorists alike. We have seen, in passing, evidence that such context-driven mechanisms do appear to occur in some species (see e.g. Belding's ground squirrels and eusocial aphids, sections 4.2 and 4.3). To understand how the evolution of context-driven social behaviour meets the inclusive fitness criterion for a given species requires an understanding of the typical ecology, demographics and contexts of interaction of that species.

The evidence for the occurrence of context-driven social behaviour in a variety of mammal species is reviewed more fully in the next chapter.

CHAPTER FIVE – THE MEDIATION OF SOCIAL BEHAVIOURS IN MAMMALS

5.1 INTRODUCTION AND OVERVIEW

Having reviewed the theoretical possibilities for 'kin recognition' (chapter 4), we are now in a position to look more closely at the expression of social behaviours in mammals. The current chapter is divided into two main sections; ecology and demographic influences and; evidence of discrimination mechanisms. At the end of the chapter, two additional sections discuss related concepts and provide an overview of what has emerged from the chapters so far.

Any investigation of what are posited to be *evolved* social behaviours has to take into account *evolutionarily typical* environments species have inhabited. As suggested in chapters two and four, ecological and demographic conditions strongly dictate evolutionarily typical contexts of interaction between individuals, including genetic relatives. The first sections of this chapter (5.2 to 5.6) discuss how basic ecological conditions have this influence on demographic patterns in mammal species. We will note that throughout varying demographic arrangements, certain contexts of interaction between genetic relatives are nevertheless reliable enough for selection to act upon. A summary of this analysis of demographic and ecological factors is given in section 5.6.

Understanding ecological and demographic influences allows a clearer appreciation of the evidence regarding mechanisms mediating social behaviours in mammals. The evidence, reviewed in sections 5.7 to 5.8, demonstrates that context-based social discriminations are overwhelmingly important in the expression of social behaviours in mammal species. These findings are summarised in section 5.9.

The *familiarity* mechanism which is widely demonstrated to mediate social behaviours requires species to engage in social learning and social recognition. Many kin recognition theorists use the concept of *social bonding* when investigating social recognition typical to close relatives in many mammal species (discussed in section 5.10). We close the chapter by noting that a distinction between *evolutionary* processes and the *expression* of social behaviours can be helpful in resolving some debates around kin recognition theory. As Kitcher (1985) suggested (chapter 3), in the human case, once we have understood the evolutionary process involved, investigation of the expression of social behaviours may be of more interest. The following chapters will turn to this question.

5.2 THE BASIC 'NICHE' OF MAMMALS

Present day mammals and their mammalian ancestors have certain basic characteristics which can be considered "facts of biology" as well founded as any (see chapter 1). Mammals are endothermic, almost all have live-birth (*viviparity*) and new-borns are often immobile and always totally dependent (socially dependent if you will) on their carer(s) for nursing with nutrient rich milk and for protection. This fundamental social dependence is a fact of life for all mammals, including humans.

Amongst other consequences these features may have served mammals early in their evolution by allowing relatively underdeveloped infants to rapidly attain adult physiology especially in regard to ecological feeding opportunities, an advantage which could have given them the edge over their reptilian dinosaur cousins in the late Cretaceous (Macdonald 1995). Over the past 70 million years, mammals have undergone rapid evolution to multiple forms and have come to dominate land-based ecological niches.

Due to the basic characteristics of mammalian reproduction, combined with demographic factors (see below) which typically isolate a reproductive female and her infant offspring, a reliable situation in which there is a statistical association of replica genes between a reproductive female and her genetic offspring exists (and has been evolutionary typical) for most mammal species. As will be illustrated in more detail below, in group-living mammals this typical fundamental association between a female and her offspring may also extend out beyond infancy.

5.3 ECOLOGICAL AND DEMOGRAPHIC VARIABLES IN MAMMALS: OVERVIEW

In his original papers on inclusive fitness theory, Hamilton discussed the potential influence of demographic factors on the patterns of statistical association of replica genes (see chapter 2). In particular, he mentioned the influence of exogamy and migration patterns on the genetic constitution of a demographic group (Hamilton 1975), and the variation in distribution of relatives (maternally related and paternally related) resulting from mating systems (Hamilton 1987).

Other relevant demographic variables include litter size (e.g. multiple or single births), birth spacing, age of weaning or independence and any sex-biased exogamy. These variables will particularly shape the grouping context of *maternal* relatives beyond the fairly constant mother-infant-offspring 'group'. Outside of the early developmental context, perhaps after weaning, there may be other situations in which *paternal* relatives are encountered. In addition to the demographic variables listed above as influencing distribution of maternal relatives, variations in mating system, and sex bias of exogamy will further influence the statistical association of paternal relatives (and replica genes). The next sections will discuss asymmetries in the distribution of maternal and paternal relatives further.

Ultimately many of these variables, as well as fundamentals such as population density, are influenced by ecological factors. Thus for a given species, an analysis of these demographic variables is typically inseparable from an analysis of the ecological niche of the species under study. The fundamental situation can be summarised thus;

> "The breeding systems of mammalian species are strongly influenced by the density and dispersion of their populations. These in turn are affected by variations in the distribution of resources. Through quantitative comparisons, it is possible to trace evolutionary relationships between feeding behaviour, population dispersion, breeding systems and morphology." (Clutton-Brock & Harvey 1978, 191)

An important influence on the initial close clustering and thus potential interaction of genetic relatives is litter-size and time between subsequent litters, variables relevant to what is traditionally known as 'r or K selection' (MacArthur and Wilson 1967), or equally treatable with 'life history theory' (Stearns 1992, Charnov 1993). What are often referred to as 'r' (resource-limited) type species tend to produce large litters at frequent intervals, whereas 'K' ('carrying capacity') type tend to have smaller litters and greater intervals between litters. These variations are considered a response to ecology, particularly the stability over time of key food resources. When prime resources are periodic and potentially highly abundant, species tend to be 'r' selected; small in body size, short lived, quick to reproductive maturity, and having large litter sizes (and potentially high mortality). Species relying on more stable food resources tend to be 'K' selected; larger, longer-lived and slower to reproductive maturity, with small litters (or single births) with a longer period of infant dependency. Time to maturity and subsequent dispersal will obviously have an influence on the opportunities for and duration of interactions between genetic relatives.

The nature and size of the minimum demographic group (from solitary female with pre-weaned offspring, to multi-female, multi-male durable groups); the patterns of dispersal from the natal-group (perhaps upon weaning or sexual maturity); the duration of interactions between individuals both within the group and after dispersal; all such variables have been studied intensively by ecologists, and here too there is agreement about the crucial impact of ecological influences such as major food source(s). Early studies uncovering the strong correlations between ecology and demographic patterns included work by Crook (1964, 1970) and Orians (1969). The latter study linked ecology and resource availability to mating system using data from bird species, but has since been found relevant in mammals also (Rubenstein & Wrangham 1986). Further work (Emlen & Oring 1977) suggested that opportunity for polygynous mating systems may be influenced by the spatial and temporal distribution of individuals of the sex dictating the basic reproduction rate; in the mammal case usually females (Trivers 1972). This complimented other studies (Jarman 1974, Bradbury & Vehrencamp 1977) suggesting that the distribution of females was greatly influenced by requirements of seeking food resources and avoiding predation and other threats. In their conclusions to their 1986 edited volume, Rubenstein and Wrangham characterised the picture thus;

> "Unravelling the evolution of any social system must begin with an understanding of the roots of female behaviour, since the behaviour of males is largely adapted to that of females. Finding these roots can be assisted by answering three queries. First, does the distribution of the critical resource (food, water, safe sites) force females to forage, travel, or live alone? If the resources are sparsely distributed, or intense predation can only be avoided by crypsis, then females will be forced to spend most of their time apart. Second, does the nature of the critical resource facilitate its exclusive defense? If territoriality by lone females is economically feasible then females will rarely meet, otherwise they may aggregate when not contesting this critical resource, and a variety of fission-fusion type social systems may develop. If females are not forced to forage, travel, or rest alone, then a third query must be answered – does the distribution of resources or the overall structure of the habitat permit females to aggregate, or force them to do so? Permissive habitats are bountiful ones where resources are distributed fairly evenly, and competition among females is low. In such situations the risks of either predation or male harassment may be so high that females aggregate around males that can provide benefits sufficient to reduce these risks and offset the cost of competition. Since competition for primary resources may be keen, permanent associations may develop. Conversely, in other habitats where resources are distributed in rich but scattered patches competition is intensified and may force females to aggregate, ensuring that others and not oneself, are excluded." (Wrangham & Rubenstein 1986, 469-470)

In short, typical demographic patterns are closely associated with ecological niche. Since this niche is different for each species, it must be investigated in any analysis of the potential for interaction between individuals (including genetic relatives). As we saw in chapters two and four (sections 2.1.6 and 4.7), an understanding of typical interaction and grouping contexts is crucial to understanding mechanisms of 'kin discrimination' and ultimately, how inclusive fitness theory might apply to a given species.

The following sections look in more detail at how demographic factors affect the potential context of grouping of genetic relatives in mammal species.

5.4 BASIC GROUPING CONTEXTS AND ASYMMETRIES OF INTERACTION

As noted by Clutton-Brock and Harvey amongst others (1978, quoted above) mating systems are a key demographic factor largely influenced by the ecological niche occupied and basic aspects of the life history of the species under study. The simplest rule that seems to hold for mating systems, with a few exceptions (such as 'leks'), is that females are distributed according to resources (and predator avoidance) whereas males are distributed according to where they can find the females. As described by Rubenstein and Wrangham;

> "[A] framework is now in place for examining how ecology shapes certain intra- and inter-sexual relationships… [I]n its simplest form, the model expects first, that female behaviour – and this includes their social relationships – will be adapted primarily to meeting demands imposed by the physical environment. This is because the reproductive rate of females will normally be raised, or lowered, more predictably by their success in meeting these demands than their success in other endeavors such as finding, or choosing among, mates. Second, it expects that male strategies are adapted primarily to competing for mating opportunities, because male fitness is more closely tied to mating success than to the acquisition of other resources." (Rubenstein & Wrangham 1986, 6)

From the brief introduction in section 5.2 (above) it should be clear that variations in mating system don't usually significantly alter the fundamental grouping context of a female and her dependent offspring. Thus, whether the mating system is polygynous (one male with several females) with isolated solitary reproductive females, or monogamous with the male and female cohabiting, female and dependent offspring are typically in close physical contact from birth. Conversely, the grouping context of paternally related individuals, both male-and-offspring and paternal siblings, is highly influenced by males' patterns of sexual activity and habitation. Immediately an important distinction emerges: Evolutionarily typical grouping contexts are rarely symmetrical between maternally related individuals and paternally related individuals. Whereas a minimal reliable grouping context is typically available for the former, for the latter, any context of interaction is more rare (since monogamy and male cohabitation with a female are rare in mammals).

The assumption of many sociobiologists (as noted in chapters 2 and 3) has been that; where the coefficient of relatedness (degree of 'r') between individuals is of equivalent magnitude, social behaviour accompanying that level relatedness is equally 'expected to be' equivalent. In particular, we found that the Darwinian anthropologists (chapter 3) assumed males *have evolved to 'parentally invest'* in their offspring according to their coefficient of relatedness. In this section we briefly look at a few examples of mammalian mating systems and the typical grouping contexts of relatives they give rise to. This will clearly demonstrate that selection pressures on the evolution of social behaviour typical to different classes of genetic relative can be quite different, even if the magnitude of the coefficient of relatedness between them is equivalent.

Although mammalian mating systems can be roughly classified into polygyny, monogamy and polyandry, these classifications tend to cross equally important demographic variables such as whether individuals cluster or are in isolation. It is also important to note that even the same species may exhibit different demographic arrangements in different environments, so flexibility is a key characteristic (especially in primate species, see chapter 6).

Polygyny (one male mating with more than one female) is much the most common mating system in mammals, but its form will vary greatly depending on other demographic factors. The most common demographic arrangement amongst mammalian species is one of dispersed and solitary reproductive females occupying their own feeding ranges (see e.g. Clutton-Brock 1989). A number of such isolated females will tend to mate with one male who maintains a (larger) local territory for comparatively short periods (usually substantially shorter than the female's residence in her territory and her reproductive span). Beyond the female-offspring group, interaction in such species usually involves a very limited bond between males and females, typically lasting only for the duration of mating itself. A further complication is that there may be other males in the area who succeed in fertilizing some females, and multiple paternity litters may even be possible (e.g. Belding's ground squirrels, see below).

Another form of polygyny occurs in species which don't have fixed territories and may congregate in groups. Some mammals may move frequently to access seasonal food sources perhaps ranging over a large, thinly distributed resource base as seen in many ungulates (Clutton-Brock 1989) and thus not have discrete home ranges (e.g. African Buffalo). Where a number of reproductive females are associated in such groups (see Wrangham & Rubenstein above), depending on breeding seasonality and female reproductive synchrony, one or a small number of males may be able to monopolise the matings with a significant proportion of females. Depending on the length of tenure of the male occupying this role in such species, and the patterns of dispersal from the group (see next section 5.5), there may be opportunities for interaction of the male and his potential offspring, or there may be no such opportunities.

A variation on the above pattern is multi-male, multi-female mating systems. Here, two or more males may regularly associate and mate with (usually a greater number of) group-living females. This pattern is fairly common in some primate species (see chapter 6).

Another possible mating arrangement is monogamy, where a single male and female will pair for an extended period, in some cases perhaps for most of their reproductive careers, and thus produce full sibling offspring. More often monogamy is limited to shorter periods, perhaps a single breeding season. Even in apparently monogamous species, depending on the degree of isolation, both partners may mate outside the pair. Mating systems where a single male is *cohabitant* with a female and her offspring are very rare in mammals (a few rodents, primates and some others).

An even rarer mating system is one where a single female will associate with a number of males for extended periods, and may mate with two or more of the males (sometimes called 'polyandry'). The males may assist in defending scarce territory and resources, and even assist in raising offspring. When this does occur, the species involved may follow a different breeding system in other ecological conditions.

Looking at mammals as a whole, the most common arrangement is that of a mature female living in isolation and mating with more than one male over her reproductive life. Other species have females living in groups, with the same breeding pattern. In both these systems maternal relatives, at minimum the reproductive female and her offspring, will be regularly associated.

Contexts of interaction of paternal relatives are typically fewer. Depending on factors such as; the size of the group of associated females; the number of polygynous males; the degree of reproductive monopolization by a small number of dominant males (reproductive skew); the length of association/tenure of any such male(s) with females; and the litter size and birth interval of the females' offspring – there may or may not be significant interaction between paternally related individuals. A further crucial variable, particularly for 'ongoing' interactions, is the pattern of philopatry and dispersal typical of a species (see next section); this also typically leads to asymmetrical distribution of paternally related individuals compared to maternally related.

Notice then that the same magnitude of 'r' (coefficient of relatedness) characterises *different classes of genetically related individuals*, (e.g. mother-and-offspring and father-and-offspring or maternal half siblings and paternal half siblings). The idea that inclusive fitness theory predicts that any individuals of a *given magnitude of 'r'* are *expected to engage in social behaviours* (such as 'male parental investment') *to the same degree* is incorrect (see chapter 2): Clearly very different opportunities for interaction will be available for paternal as compared to maternal relatives. This error was a key unresolved issue in the Darwinian anthropological reading of inclusive fitness theory.

Even amongst those interpreting inclusive fitness theory as a description of selection pressure on genes, there has been a tendency to overlook the point that selection acts on the expressed effects of genes, and behaviours statistically associated with the presence of those genes (Price 1970). For example, it has sometimes been assumed that, because genes pass through males and females in subsequent generations, and thus are for the most part statistically equally likely to have derived from a 'mother' or a 'father', a gene should be equally strongly selected for its inclusive fitness effects (and behaviours promoted) towards maternal siblings (perhaps clustered) as towards paternal siblings (perhaps likely to be more widely dispersed). In other words, an assumption has been that 'inclusive fitness' will mould genes *to have effects which are* 'symmetrical' on relatives, whilst ignoring the demographic potentials provided for contexts of interaction. This too reflects a mistaken teleological understanding of inclusive fitness theory. A gene's expression may tend to have certain effects, and whether some of these effects might amount to being 'social' (in the sense described in chapter 2) depends on the demographic context. If an interaction context is present, it is such effects as these which (initially randomly arising) are then acted on by selection pressure to meet the inclusive fitness criterion. There are few kinds of effects that could possibly have the same consequences for all the variously different classes (both maternally and paternally related classes) of a given magnitude of relatedness under circumstances where the typical distribution patterns of such individuals is entirely different.

Where effects are asymmetrical, it might be that a gene's having positive impact on replicas in maternal relatives (when maternally derived) entails having a potentially negative impact on replicas in paternal relatives (when paternally derived). So long as the positive consequences in the former occasions outweigh the negative consequence in the latter, these effects will nevertheless meet the inclusive fitness criterion. Haig (1997) gives a more formal presentation of this point, and quantifies the selection pressures involved.

5.5 ADDITIONAL INFLUENCES; PHILOPATRY AND DISPERSAL

In most species of mammals, females give birth to more offspring than the population replacement rate. Apart from occasions with high short-term abundance of resources (see 'r selected' species, above) the finite local environment cannot support all offspring produced by all females, and thus some degree of dispersal from the natal territory/homerange is inevitable. Unless resources within the wider environment can support a growing population, initial dispersal ('natal dispersal') will not necessarily result in survival nor successful settling and breeding, and thus further moves, or what is known as 'breeding dispersal' into subsequent territories may be necessary (e.g. Belichon et al. 1996, Clarke et al. 1997, Paradis et al. 1998). Inevitably, dispersal typically involves significant risks (e.g. Motro 1991, Alberts & Altmann 1995). However, remaining within the natal environment may also involve risks, particularly in environments with variation in resource availability (e.g. McPeek & Holt 1992, Johst & Brandle 1997, Mathias et al. 2001).

Apart from such resource pressures, there are further selection pressures on the evolution of dispersal. Inbreeding avoidance between closely genetically related individuals may promote dispersal (Clutton-Brock 1989, Pusey & Wolf 1996, Perrin & Mazalov 2000) to avoid potential inbreeding depression (Lacy 1997, Crnokrak 1999, Keller & Waller 2002).

Particularly for 'K selected' species (see 5.3 above) in which stable local environments may allow a proportion of individuals to remain in their natal range, inbreeding avoidance, mating competition and resource competition in general tend to produce sex-biased dispersal. Which sex of offspring typically remain and which disperse depends on the relative costs/ benefits to the sexes, and the wider ecological pressures on the resource/ territorial options of the sexes in general (Clutton-Brock 1989, Johnson & Gaines 1990, also see Rubenstein & Wrangham 1986, above). We have already seen that, in mammals, female access to resources tends to dominate the fundamental demographic patterns. Whereas in birds, dispersal is often female biased, since males engage in resource competition for successful mating opportunities (reviewed in Johnson & Gaines 1990), in mammals, due to resource competition, females usually (but not always) remain in the natal territory for resources (are 'philopatric'), and males tend to disperse for mating opportunities (Wolff 1992, Altmann & Alberts 1996, Isbell & VanVuren 1996).

Patterns of philopatry and dispersal greatly influence the genetic relatedness of individuals who remain in their natal range, and this will be particularly significant in group-living species, as we will see in the review of primate species, in chapter six.

5.6 ECOLOGY AND DEMOGRAPHICS SUMMARY

As suggested in chapter two (section 2.1.6 and see Sherman 1980), the ecological niche a species occupies, and the associated demographic patterns typical of it are fundamental to an analysis of the potential for social interaction and social behaviour, and an understanding of how social behaviour might be mediated.

In particular, typical grouping contexts of genetic relatives will vary with demographic factors such as group-living or isolation, polygynous mating system or monogamy, and male or female dispersal. Further factors will influence typical grouping contexts and patterns of interaction between genetic relatives. Litter size and time to maturity will influence the statistical association of genetic relatives such as a female and her offspring, or the offspring themselves. The interaction between the female and her offspring is highly statistically reliable in isolated living mammal species, as noted above. In species with large litters, a number of maternal siblings will typically interact in close proximity with the reproductive female during infancy. In species with long infant dependency and single births, maternal siblings from subsequent gestations may also interact, in the presence of the nursing female. In species where females aggregate and group membership is highly durable (Wrangham & Rubenstein above), and where young male offspring disperse from the natal group at reproductive maturity, whilst young females remain, extended association of related reproductively mature females is a consequence.

In chapter two (section 2.1.6) it was suggested that the various distinct grouping situations an individual may encounter (e.g. in the nest/burrow versus on the edge of the territory) will typically be comprised of individuals of concomitantly different degrees of genetic relatedness. The following sections will illustrate how, for many mammals, context-dependent cues mediate the expression of social behaviours, and how these reliably correlate with the typical demographic environments that individuals of a given species might encounter.

5.7 EVIDENCE ON MECHANISMS MEDIATING KIN DISCRIMINATION IN MAMMALS

The typical patterns of interaction analysed in the last section demonstrate that certain reliable contexts are available to mediate context driven recognition in many mammal species. For grouping contexts (and social behaviours) relevant to many types of genetic relatives, simple continuities from birth can potentially mediate 'recognition'. The case of paternal half-siblings is an exception here since a common context at birth does not necessarily exist, yet individuals may encounter one another later in development. Where such encounters have potentially significant outcomes, self-referent phenotype matching (see chapter 4.6) may be the only means to mediate 'recognition'. This will particularly be the case where no other context-driven-cues (such as membership of a cohesive social group) are reliably statistically associated with common paternity; particularly in species where a male's matings are more widely scattered such that even geographic proximity cannot serve as a reliable cue to common paternity. Of course, in such cases, opportunities for significant interaction (and selection pressure upon social behaviours that meet the inclusive fitness criterion) would also be correspondingly slight. However, 'recognition' for purposes of inbreeding avoidance might still be selected for (see Hamilton 1987, chapter 4.5).

The following sections briefly review the relevant evidence for the respective occurrence of context-based recognition and 'positive powers' of recognition in mammals. Holmes (below) gives a succinct account reminding us of the relationship between ecological niche, demography and selection pressures. He goes on to summarise the kinds of recognition which appear to operate (or be absent) between different types of genetic relatives in the much studied Belding's ground squirrels (*Spermophilus beldingi)*;

> "If parental ability to discriminate own offspring has evolved in both sexes, females and males will often rely on different proximate mechanisms to make discriminations… males in most mammalian species are unlikely to rely on the association mechanism in nature because, at the proximate level, they rarely interact directly with their young during early development... In polygynous, polyandrous or promiscuous mating

> relations, or when mate guarding by males is often unsuccessful, three recognition mechanisms other than prior association might facilitate father-offspring recognition. First "mediated recognition" [via association with the mother]… Second, if male's offspring were predictably and reliably distributed in space, differential treatment of male's own and alien young would occur if males varied their behaviour relative to location cues… if females reared their litters in the territories of males they mated with and males protect young within males' territorial boundaries, then sires would be treating their own offspring preferentially as a result of location specific behaviour… a third mechanism that males could employ to recognise offspring is phenotype matching." (Holmes 1990, 447-449)

> "Three points suggest that male *S. beldingi* do not recognise their offspring. First, males do not behave parentally toward young, regardless of male-young relatedness. Second, males leave the meadow areas where they inseminated females shortly after mating (Sherman & Morton, 1984) and thus do not interact with the juveniles they sired. Finally, because most litters are of mixed paternity due to multiple mating by females (Hanken & Sherman, 1981), the identities of a male's former mates, even if he could recall them, would not correlate with male-young relatedness." (Holmes 1990, 450)

Holmes also sums up the evidence regarding female-offspring 'recognition' mechanisms in this species;

> "Mother–offspring recognition in *S. beldingi* is based on the association mechanism, as revealed by field (Holmes & Sherman, 1982) and laboratory (Holmes 1984) tests (see also Mitchner & Sheppard, 1972, and Mitchner, 1974, on Richardson's Ground squirrels). In the field, Sherman found that he could foster alien young by placing them near natal burrows and waiting for resident dams to retrieve them. When litters later emerged, resident dams treated their biological and foster offspring alike and behaved aggressively towards young reared by other (unrelated) females. In the laboratory, Holmes fostered young reciprocally between females shortly after birth and later found that dams retrieved 22-day-old young they had reared (familiar young) faster than young they had not reared (unfamiliar young). Retrieval times did not vary with true relatedness (Holmes 1988, fig 3). Thus in field and laboratory tests, *dams responded not to their biological offspring as such, but to familiar and unfamiliar young*. Because dams *in nature* rear their young isolated in underground burrows until the young are weaned, *a "familiarity rule" (learn kin signatures of the young in your*

> *burrow) would result in discriminate treatment of a dam's own offspring*." (Holmes 1990, 451, emphasis added)

In fact, as well as this very striking support for a context-based familiarity mechanism operating in *S. beldingi,* in all species that have been *successfully cross-fostered*, this in itself is strong *prima facie* evidence that a context-based rule is operational in the mother-offspring case (further examples given below). In the case of the 'recognition mechanism' operating in infants themselves;

> "*S. beldingi* young (1) can distinguish between the dam that reared them and the one that did not, (2) *behave as though they cannot recognise their biological dam if reared apart from her* (3) distinguish between a familiar and an unfamiliar dam at about the age young could first come above ground in the field." (Holmes 1990, 452, emphasis added)

As for sibling-sibling recognition, Sherman et al. (1997) summarise the findings;

> "Female Belding's ground squirrels learn kin recognition cues from nestmates. In this species, mothers and daughters and sisters behave nepotistically: they warn each other of predators and protect their own and each others' pups against infanticide by establishing and jointly defending territories (Sherman, 1977, 1981a,b). Cross-fostering studies in the field (Holmes & Sherman, 1982) and laboratory (Holmes, 1984, 1986a, 1994) indicate that nestmate females learn each others' odours just before weaning (when litters normally begin to mix), and later treat each other as siblings, *regardless of actual relatedness*. Socially learning these kin-recognition templates does not increase acceptance errors in nature because unrelated pups rarely cohabit the same nest burrows." (Sherman et al. 1997, 82, emphasis added)

But Sherman et al. note that there is some evidence that this context driven recognition, though primary, may be slightly supplemented by self-referencing in the case of paternal half-siblings, and point to the mating system as a factor;

> "Female Belding's ground squirrels mate with one to eight males and most litters are multiple sired (Hanken & Sherman 1981). In the field,

> females are slightly less likely to attack full-sisters than maternal half-sisters, and more likely to share territories with full-sisters (Holmes & Sherman, 1982). Discrimination of nestmates from non-nestmates and full from half-sisters among nestmates suggest that a female's own smell, as well as the odours of nestmates, both contribute to her kin-recognition template (Sherman & Holmes 1985). In apparent support of self-referent phenotype matching, in laboratory studies paternal half-sisters also recognised each other (Holmes 1986b; but see Alexander, 1991)." (Sherman et al. 1997, 83)

Alexander (1991), mentioned here by Sherman, simply notes that the 'template' (see 4.4) used for recognising relatedness in the case of unfamiliar paternal siblings in this species could in fact have been learned from litter-mates who shared the same father (Alexander 1991, 387) and thus context-based recognition may play a part in mediating the effect.

Similar results emerged with a related species; Holmes (1995) found that in Golden-Mantled ground squirrels *Spermophilus lateralis*, cross-fostering experiments suggested that a shared environment of co-rearing (in the lab) with a nursing female had more influence on subsequent social preferences (in a semi-natural environment) than being genetic litter-mates *per se*. However, the latter did exert some effect, such that the overall preference for social interaction, as measured by play-bout frequencies was ordered: litter-mates reared together>non-litter-mates reared together>litter-mates reared apart>non-litter-mates reared apart (Holmes 1995, 309).

Hare (1992) conducted dyadic interaction tests on wild Columbian ground squirrels *Spermophilus columbianus* and found that similar levels of cohesion and hostility were exhibited by all intra-colony dyads. Conversely, interactions between members of different colonies demonstrated lower cohesion and increased hostility. These results suggest that there may be a group-member familiarity mechanism at work (Hare 1992). Later cross-fostering work (Hare & Murie 1996) found that;

> "Rearing association significantly influenced recognitive and agonistic behavior among juveniles while relatedness proved insignificant in affecting behavioral interactions. Thus, direct familiarization in the natal burrow is both sufficient and necessary to account for the transitive

> appearance of kin-differential behavior among newly emerged juveniles documented in previous studies." (Hare & Murie 1996, 76)

Hare (1998) has also conducted work on Richardson's ground squirrels, *Spermophilus richardsonii* which also suggests that the ability that juveniles develop to discriminate between neighbours and strangers is based on familiarity.

Heth et al. (1998) found evidence that golden hamsters, *Mesocricetus auratus,* can distinguish between siblings and non-siblings based on scent cues despite successful cross-fostering, which they suggest may reflect a self-referent phenotype matching ability. However, no positive social behaviours (discriminations) other than the individuals' own scent-marking behaviour (linked to inbreeding avoidance in females) were demonstrated to accompany this recognition ability.

Sun and Muller-Schwarze (1997) found that the beaver, *Castor canadensis,* displayed a similar ability to distinguish between the scents of related and unrelated individuals in the field, and show stronger territorial response to the scent of non-relatives, which suggests self-referent phenotype matching. They also note that an individual's mate also responds differently to the scent of its partner's relative, demonstrating phenotype matching via learned familiarity.

Tai et al. (2000), whilst analysing the inbreeding avoidance cues of the mandarin vole, *Microtus mandarinus* found that co-habitation during development plays the key role on subsequent mate choice, although there was an slight, non-significant, role for genetic relatedness. They thus suggest that in this species "genetic relatedness may have some effect on kin recognition, although familiarity is the main mechanism." (Tai et al. 2000, 2119).

Stookey and Gonyou (1998) conducted cross-fostering experiments on pigs, *Sus scrofus,* to measure the comparative effect of familiarity or genetic relatedness and measured no detectable decline in aggression between sibling dyads reared apart over non-familiar non-siblings. Conversely, familiar non-siblings (reared together) spent significantly less time fighting than those reared apart. Based on these results, they suggest that "recognition among young piglets appears to be based on familiarity gained through rearing associations, and does not involve genetic relatedness" (Stookey and Gonyou 1998, 291).

In a recent review, Hauber & Sherman (2001) describe only two cases in which they believe self-referent phenotype matching has thus far been clearly demonstrated in mammals, one being golden hamsters (see Heth et al. 1998 above), the other being Alberts' work on baboons (see next chapter).

The overall impression from these studies is that *context-dependent* discrimination, and *learned* recognition, are unambiguously the most influential mediators of social behaviours for most mammal species tested. Waldman's (1988) review gives a useful montage of the recognition mechanisms documented in mammals;

> "Social systems of many mammals tend to be matrilineal in character, as the female parent is the primary care provider. In rodents (e.g. gerbils, *Meriones unguiculatus),* discrimination of young is facilitated by salivary cues the mother applies to her offspring (28). Similarly, goat mothers label their offspring by licking them (89). Sheep dams recognize their lambs by visual and auditory cues from a distance and by smell at close range, and lambs recognize the individual calls of their mothers (175). Many ground-dwelling sciurids rear their litters in their own burrows, so social groups consist of siblings only and kin identities can be learned (155). Females of colonially nesting sciurids (black-tailed prairie dogs, *Cynomys Zudovicianus)* appear to recognize their offspring only indirectly and fail to discriminate their own young from unrelated littermates (107, 11 1). Mexican free-tailed bats *(Tadarida brasiliensis mexicana)* also nest colonially but do selectively nurse their own young and may mark their pups with odors to facilitate recognition; pups, however, do not discriminate between their mothers and other lactating females (90). Primate infants (e.g. squirrel monkeys, *Saimiri sciureus)* recognize and orient toward their mothers by olfactory cues (120). Male vervet monkeys *(Cercopithecus aethiops)* exercise parental care as well, for example, responding to infant distress calls (98). Paternal recognition appears to be circumstantial, however, as males provide parental care to offspring of females with which they had consorted during the approximate time of conception (39, 79, 98)." (Waldman 1988, 545-546, see references in original)

5.8 SELECTION AGAINST CLEAR SIGNALS OF RELATEDNESS

Waldman (above) notes that, in primates, “paternal recognition” and protection of infants appears mediated via familiarity with the female (see next chapter for more detail). Note that, particularly relevant to male-infant interactions, there may be species for which positive selection exists upon obscuring accurate cues of actual genetic identity, for example, where non-relatedness would result in costly rejection (or worse). Sherman et al. illustrate this point;

> “[W]hen recipients benefit from the absence of discrimination they will be favoured to hide their true kinship by ‘muting’ or ‘scrambling’ recognition labels (Reeve, 1997a). For example, extrapair copulations set in motion a coevolutionary arms race between males attempting to discriminate their progeny and unrelated juveniles attempting to dupe the male by not revealing their genotype via their phenotype (Beecher, 1981). If young are initially uncertain about whether the resident male is in fact their father, they should hide, change or mix their recognition cues (e.g. via rapid growth and feather development) because the fatal cost of being rejected, even if improbable, may exceed the small benefit, even if likely, of receiving extra food from a male that has identified them as his progeny. Juveniles have an upper hand in this coevolutionary struggle because, on average, they have more to lose by being recognised and rejected than males lose through misdirected nepotism.” (Sherman et al. 1997, 93)

Pagel (1997) has made a similar point, and has formalised the argument in a model demonstrating that comparatively few instances of actual non-relatedness could exert selection pressure upon concealment of relatedness;

> “[A] simple population genetics model shows that some aspects of neonatal appearance may arise as adaptive strategies on the part of infants actively to conceal the identity of their parents, especially of their father. Concealing paternal identity is advantageous as a strategy to avoid paternal neglect, abuse, or infanticide when the ‘domestic father’ is not likely to be the ‘biological father’. The model reveals that ‘anonymity’ as a neonatal strategy can be adaptive in a wide a variety of mating systems, because infants are expected to resemble their fathers only if the ‘domestic father’ is also the ‘biological father’ a high proportion of the time. Even small

> amounts of paternity uncertainty are sufficient to select against parent-infant resemblance." (Pagel 1997, 973)

Pagel goes on to discuss whether the model may be applicable to the human case, but provides little by way of discussion of possible selection pressure in past environments. Nevertheless, the point remains that signalling genetic identity may be selected against in species where unrelated individuals may be in a position to withhold care, or exert harm on infants on the basis of cues of their actual genetic relatedness. There are many species where this power imbalance exists, as illustrated by Waldman;

> "Male lions *(Panthera leo)* kill new cubs in prides that they have just taken over, and as in rodents, females generally become reproductively receptive more quickly, thus allowing the intruder males to breed (170). Recent immigrant male *Colobus* and *Procolobus* monkeys similarly kill unrelated infants, and this pattern is typical of the nonhuman primates (211). Mammalian studies reveal in general that males refrain from killing infants in social circumstances in which they potentially might have fathered those individuals. Only rarely does kin discrimination appear to be more precise, and then males assess their paternity by using cues of the mother rather than the infants themselves (99). For example, male mice *(Mus musculus)* kill their own offspring when they are placed in the nest of a strange female, but they tolerate offspring they have not fathered that are placed in a familiar female's nest and those that may be marked with urine odors of familiar females (114)." (Waldman 1988, 554)

These considerations will figure more in the following chapter where male-infant interactions in primates are reviewed and discussed. Notice also that signalling actual genetic relatedness as a cue mediating the expression of social cooperation and acceptance within a social group may also be selected *against* in species in which such social solidarity is vital for an individual's survival (e.g. Kokko et al. 2001).

5.9 SUMMARY: THE IMPORTANCE OF FAMILIARITY IN MEDIATING SOCIAL BEHAVIOURS

In characterising the expression of social behaviours in mammals as a whole, a distinct trend is visible. Although it is clear that a few cases exist where a positive power of discrimination (apparently self-referent phenotype matching) occurs between paternal half-siblings, the significance of this in mediating actual social behaviours (as opposed to inbreeding avoidance) appears very slight for mammals as a whole. On the other hand, even in those cases where 'positive powers' are observed, the importance of context-based discrimination, particularly the role of familiarity in mediating actual social behaviours appears unequivocal. Put differently, even in those species which do display some positive powers under experimental conditions, familiarity appears to mediate social behaviour independently of actual genetic relatedness. Waldman (1988) discusses the comparative influence of context-driven cues, particularly familiarity, and 'positive powers' of discrimination, in a range of both invertebrates and vertebrates, whether for inbreeding avoidance or social mediation. His work reaches a similar conclusion about the primacy of context-driven and familiarity cues mediating the role of social behaviour in the species' natural environments;

> "Evidence that individuals discriminate kin that they have not previously encountered, or discriminate between different classes of kin and nonkin that they have always encountered together, holds particular fascination for behavioral ecologists. In the majority of cases in which kin biases are apparent, kinship is confounded with other variables, particularly familiarity and spatial distribution. Yet the "cleaner" experimental design afforded by these studies allows kinship effects to be examined separately from those associated with other types of social interactions. Many organisms can discriminate unfamiliar kin, or among familiar kin and nonkin (e.g. 27, 75, 83, 105, 106, 121, 166, 222) [but see Hauber & Sherman 2001, above]. Yet in natural conditions kin discrimination is often based on familiarity and spatial distribution, and these cues can serve as reliable indicators of kinship identity. Experimental studies generally show that even if organisms can discriminate kin from nonkin when familiarity and proximity provide no basis for discrimination, these cues when available strongly influence behavioral tendencies. For example, individuals experimentally reared in social isolation may discriminate kin from nonkin (e.g. larvae of the amphibians *Bufo americanus* and *Rana cascadae),* but if reared in a socially mixed environment they fail to discriminate between familiar kin and nonkin (27, 166, 222). Similarly, results of several studies on rodents suggest that individuals can discriminate between unfamiliar siblings and unfamiliar non-siblings (or half-siblings), but in usual conditions these effects are masked by much

> stronger preferences to interact with familiar individuals even if they are nonkin (83, 121).” (Waldman 1988, 560)

Erhart et al. (1997) also give an overview of mechanisms mediating social behaviour in mammals and similarly characterise the overall picture as one where familiarity is of overriding importance;

> “The most widespread and important mechanism for kin recognition in mammals appears to be familiarity through prior association (Bekoff, 1981; Sherman, 1980). During development, individuals learn and respond to cues from the most familiar or most commonly encountered conspecifics in their environment. Individuals respond to familiar individuals as kin and unfamiliar individuals as nonkin.” (Erhart et al. 1997, 153-154)

Bekoff also emphasises, like Waldman, that it is familiarity which can override the presence or absence of actual relatedness in the expression of social behaviours, and not the other way round;

> “Mammalian young are born into a wide variety of social situations, ranging from being isolated from all other individuals except their mother (and possibly other siblings) to being born into large social groups. Although siblings do interact in a wide variety of species having different life histories, there are certain conditions, almost all of which have to do with the developmental environment, that will favor a biased occurrence of interactions between littermates and/or different-aged siblings. It will be argued later that it is these, and perhaps other, conditions that *predispose* (in a probabilistic way) siblings to interact with one another. However, if two (or more) very young unrelated individuals (assume conspecifics for simplicity) are exposed to these conditions, they too will behave like siblings. That is, although [relatedness] and [familiarity] are tightly linked in many mammals, it is [familiarity] that can override [relatedness], rather than the reverse.” (Bekoff 1981, 309)

We saw in earlier chapters (2, 3 and 4) that an attentiveness towards *proximate* mechanisms of social behaviour needs to accompany theoretical discussions of their *evolutionary* emergence, and particularly derivations of theory towards behavioural models. If a social context is ecologically possible for a species, whether social behaviours correlate with relatedness *via context-based cues* or *via positive powers of recognition* needs to be considered. I have argued that the former is more theoretically parsimonious. Certainly theory does not suggest that proximate mechanisms of social behaviour require genetic relatedness *per se* to be present.

In reviewing experimental evidence for the role of 'kin recognition' in this chapter, the evidence clearly points to context-based cues such as prior familiarity mediating the expression of social behaviours in the great majority of mammals studied. Combining this result with the theoretical discussion and review of earlier chapters, we can provisionally conclude that it is entirely erroneous, both in reference to theory and in reference to the evidence, to claim or suggest that 'the facts of biology' support *the claim that organisms have evolved to cooperate with genetic relatives per se*. The further question then is; can we uncover in any greater detail how familiarity and other context-dependent cues operate?

5.10 SOCIAL LEARNING AND SOCIAL BONDS

For familiarity to mediate social behaviour requires social learning during various stages of an individual's development. An emphasis on social learning can be traced back to Hamilton's original papers (Hamilton 1964) and beyond.

> "Generally, numerous workers have stressed the importance of including development in analyses of behaviour (Lehrman 1953; Tinbergen 1963; Lorenz 1965; Bekoff & Byers 1985; Alessandro et al. 1989; Byers & Bekoff 1990; Kitcher 1990)… ontogenetic variables are important in the acquisition of kin recognition in animals ranging from insects to primates, including humans (Fletcher & Mitchner 1987; Hepper 1990)." (Byers & Bekoff 1991, 1088)

Recall Hamilton's references (section 2.2.4 for full quote) to studies of the context-mediated social learning of offspring identities in birds;

> "[I]t seems a reasonable hypothesis that the ability to discriminate 'own young' advances in step with the chance that without such discrimination strange chicks would be fostered and the benefits of parental care wasted on unrelated genes. Supporting this hypothesis are the findings quoted by Tinbergen of Watson and Lashley on two tropical species of tern: 'the

> Noddies nesting in trees do not recognise their young at any age, whereas the ground-nesting Sooties are very similar to herring gulls in that they learn to recognise their own young in the course of four days.' House sparrows will accept strange young of the right age placed in the nest but after the nestlings have flown 'they will not, in normal circumstances, feed any but their own young.'" (Hamilton 1996 [1964], 53-54)

Tang-Martinez, in a recent review of kin recognition theory also notes the importance of developmental context in both learning of offspring identities by adults and in learning of adult identities (via 'imprinting') by neonates, both in birds and in mammals;

> "Developmental studies can also provide insights into the evolution of kin recognition mechanisms. In several species, the neonatal central nervous system has evolved to be particularly sensitive to learning cues that are later used to discriminate kin from non-kin. For example there are imprinting or imprinting-like processes that result in the learning of relevant cues during certain stages of ontogeny. Filial imprinting, using visual cues, is well known among precocial birds… Among rodents, neonatal learning of cues associated with the mother are also important for kin discrimination… Not all sensitive periods for learning kin-related odors occur in neo-natal animals. Female goats, Capra hircus (e.g. Klopfer and Gamble, 1966), and sheep, Ovis aries (Poindron and Levy, 1990; Kendrick et al., 1992) appear to be predisposed to learn the odors of their newborn offspring immediately after giving birth… it is well known that mothers can be deceived into accepting alien young (non-kin) as long as they are introduced immediately after parturition (Levy et al., 1991)." (Tang-Martinez 2001, 33)

Where social learning of an individual's identity leads to close familiarity which endures over time and is accompanied by particular social responses and social behaviours, the concept of a 'social bond' may be useful. Gubernick's influential *Parent and Infant Attachment in Mammals* gave an early review (1981) of the development of social bonds between relatives, and links social bonding and attachment to discriminatory parent-offspring social behaviour;

> "Parental care is one strategy which helps ensure the survival of offspring and thereby enhances the parents' reproductive success (see Klopfer, this volume; Pianka, 1970). In mammals, parental care usually involves

> behavioural interactions between parents and offspring. One form these interactions can take is that of parent and infant attachment, the subject of this chapter.
>
> The interactions between parents and offspring that have received the widest attention have been those between the mother and her young, while male parental care has been less studied… My emphasis here will be placed on mammals other than humans. Three general questions will be addressed: what is attachment, where is attachment found, and why are attachments formed?… Typically attachment is defined as a special affectional relationship between two individuals that is specific in its focus and endures over time… The important features of such definitions are (1) the formation of a special emotional relationship (i.e., affective bond), (2) with a specific individual (i.e. the specificity of the bond), (3) towards whom certain responses are directed rather than towards other individuals (i.e., differential responding). These features assume the recognition and discrimination of the attachment figure from other figures." (Gubernick 1981, 243-244)

Just as Hamilton noted the variations in the form of social learning in different bird species, so Gubernick also emphasises that the development of social attachments will depend on the typical demographic features of the species, especially the typical circumstances in which parent and infant(s) are in contact;

> "The ultimate function of attachment (measured in term of fitness) is probably not protection from predation as some have argued but rather insurance that care is provided for one's own young and not those of another. Since the same ultimate and proximate consequences are, in some species, achieved without forming attachment, it is necessary to assess the conditions favouring the evolution of parent and infant attachment.
>
> Based on the assumed function of attachment, predictions can be made regarding the likelihood of finding attachment under varying conditions of mobility of the young and social structure. A survey of the available evidence suggests that attachment does in fact occur where the chances of misdirecting parental care seems high.
>
> Although parent and infant attachment is found in many species, the mechanisms and developmental timing of such attachments may differ, as illustrated in several species of rodents, primates, and ungulates." (Gubernick 1981, 288)

Primate demography, social interactions and social bonding will be covered in greater detail in the following chapter (Chapter 6). As well as the many mammals reviewed by Gubernick, other studies of the context-based formation of social bonds and accompanying social discriminations have been conducted. These include work on rodents (e.g. gerbils; Valsecchi et al. 1996; guinea pigs; Janzen et al. 1999, Jackel & Trillmich 2003; rats; Sigling et al. 1998), ungulates (e.g. sheep; Porter et al. 1991, Romeyer 1993, Gonzales & Goddard 1998; goats; Romeyer & Poindron 1992, Hernandez et al. 2002; bison; Green 1993; horses; Houpt 2002), canids (e.g. dogs; Mekosh-Rosenbaum et al. 1994, Topal et al. 1998), felids (e.g. cheetah; Ruiz-Miranda et al. 1998), and pinnipeds (e.g. harbour seals; Lawson & Renouf 1987; sea-lions; Hanggi et al. 1990) amongst others.

In short, in those mammals where social bonds typically form between parent and infant, it is possible to investigate 'discriminatory' social behaviour via an investigation of the process of formation of those social bonds which are well established as mediating social behaviours in many species. Although clear social bonding is not inevitably present in all mammals, when we review primates (chapter 6), it is common to find that behaviours relating to 'kin recognition', 'social learning', and 'social bonding', are usually somewhat interdependent and are thus studied together. Since the development of social bonds is well established in many mammals – particularly in primates and humans – an analysis of this area becomes an efficient way of investigating the proximate mechanisms of 'kin discrimination'.

5.11 SUMMARY: CORRELATIONS AND THE DISTINCTION BETWEEN EVOLUTION AND EXPRESSION

Reviewing his own results suggesting familiarity may mediate female-offspring 'recognition' in Belding's ground squirrels (*Spermophilus beldingi*), Holmes (1990) suggests that;

> "Two points emerge from this study (Holmes, 1984). First, a kin recognition mechanism based on social learning does not allow assessment of kinship or genetic relatedness *per se*, but allows an individual to behave as though it can assess relatedness in species-typical

> circumstances. Thus "kin recognition" could more precisely be called "kin-correlate recognition," where the factor(s) correlated with kinship (rearing association in the previous example) vary with the ecology and social organisation of the species being considered (Holmes & Sherman, 1983)… Second, recognition mechanisms are best considered "rules of thumb" or "behavioural heuristics" that typically, but not always, result in kin-differential behaviour." (Holmes 1990, 442)

In this chapter, we have reviewed evidence that makes it clear that genes whose effects are 'social' can – in many circumstances, in many mammalian species – meet the inclusive fitness criterion simply by the expression of social behaviours being context sensitive. As Kitcher (1985) pointed out (see chapter 3.5) those making reference to inclusive fitness theory in applications to humans have largely *ignored the possibility of a contextual rule of thumb* by which the expression of social behaviour traits has evolved to meet the covariance criterion of inclusive fitness. Instead it has been assumed that inclusive fitness theory must involve the notion that the expression of human social behaviour will *actively target* genetic relatives essentially by 'recognising kin' *per se* and differentially interacting with them. Based on the evidence reviewed in this chapter, for this to be true would require that the expression of social behaviour in humans has evolved to be totally different from that seen in all other mammals. The plurality of cases in which social behaviours are mediated by familiarity and context-based cues which in evolutionarily typical contexts have "correlated with kin" (Holmes, above), demonstrate that Darwinian anthropology's assumptions that *genetic relatives are actively targeted* to be false interpretations of the theory. Such evidence also raises questions over the utility of the concepts relating to *kin recognition* to the extent such concepts are understood to be core predictions of Hamilton's theory, since there is no clear basis to the claim of that positive powers of discrimination are necessary to mediate *inclusive-fitness-type* social behaviours;

> "[T]he fact that animals benefit from engaging in spatially mediated behaviors is not evidence that these animals can recognise their kin, nor does it support the conclusion that spatially-based differential behaviors represent a kin recognition mechanism (see also discussions by Blaustein, 1983; Waldman, 1987; Halpin 1991). In other words, from an evolutionary perspective it may well be advantageous for kin to aggregate and for individuals to behave preferentially towards nearby kin, whether

> or not this behaviour is the result of kin recognition *per se*." (Tang-Martinez 2001, 25)

As we saw in chapter four (4.3), theorists such as Tang-Martinez and Grafen (1991) have questioned the concept of 'kin recognition' on this basis. Such considerations led Grafen to suggest that we might want to limit the 'kin recognition' concept strictly to cases where 'positive powers' of discrimination are used. It may be helpful to recall that theories about evolutionary selection pressures are necessarily about *typical* outcomes of the effects of genes. Genes and behaviours spread (increase in frequency) simply because of their statistical covariance (Price 1970) with reproductive success in the species' typical environments. Thus a selection criterion relevant to *evolutionary* trends does not entail that the *expression* of social behaviour must be contingent on actual genetic relatedness *per se*. Failing to note this distinction between the *evolutionary* process and the *expression* of behaviours can lead to confused debates. For example, others theorists respond to Grafen's (1991, see section 4.3) point (which is really a call for caution over theorising about what might mediate the expression of social behaviour) with the opposite emphasis, suggesting that 'kin recognition is what kin recognition does'; in other words a focus on evolutionarily-typical statistical outcomes;

> "I suggest that group or individual recognition systems might well qualify as kin recognition regardless of the cues used, provided that the groups or individuals so recognised are routinely kin and that the fitness benefits associated with recognition typically flow among kin… Grafen's insistence that kin recognition be a function of genetically based cues and that no individual or group recognition system should qualify excludes many recognition systems that may well function to associate kin in a fitness enhancing context. Kin recognition is an inherently functional concept and any definition or restriction that relies too much on a particular mechanisms or source of cues is problematic." (Stuart 1991, 1093)

Of course both sides of the debate are right, but are really talking about two different things; evolution and expression. It could be argued that this tension between emphasising *evolution* or *expression* has dogged kin recognition research and theory for a long time. On the one hand it makes sense from the perspective of analysing 'function', i.e. evolutionarily significant statistical outcomes, to be plural in classifying the mechanisms/ processes/ circumstances that potentially mediate kin discrimination. On the other hand, if we want to strictly understand the ontogeny and flexibility of potential for an individual's *expression* of behaviours which lead to social bonding and social behaviours, it is vital to approach 'kin recognition' with a view to proximate mechanisms of expression, and bear in mind the typical correlation of such 'rules of thumb' with bonding and behaviour between genetic relatives in typical evolutionary environments. As Tang-Martinez puts it;

> "Some may argue that this criticism [should kin bias be considered 'kin recognition'] is irrelevant if one is interested primarily in the evolutionary consequences of behavior. This may be true, but it begs the question of the underlying cause of the behavior. A lack of knowledge, or a misunderstanding, of the proximate mechanisms of behavior can lead to erroneous conclusions about evolution and function… In summary, it is not enough to argue that the consequences of a behavior (e.g. kin bias) may be adaptive and that is all that matters in the long run. To adequately understand the behavior and the evolutionary forces that have influenced it, it is imperative also to understand the underlying processes and mechanisms that have given rise to the behavior." (Tang-Martinez 2001, 25)

This is particularly the case with analyses of human social bonds and behaviour. Without a consideration of the evolutionarily typical environments in which behaviours evolve, references to *inclusive fitness* are not only potentially misinterpretations, but also might contribute little to our understanding of the proximate workings of social behaviour. As we noted in chapter three (3.5 for full quote), Kitcher made a very similar point to that of Tang-Martinez, about Darwinian anthropologists' hypotheses;

> "Let us suppose that Alexander, Kurland, and others succeed in showing that in certain environments particular forms of social behaviour maximise the inclusive fitness of those who engage in them. What exactly have we learned about human nature?" (Kitcher 1985, 282)

If the expression of social bonding and behaviour in humans has evolved to be context-based, via an historically reliable context of interaction between actual genetic relatives, the same social bonding mechanisms could readily lead to social bonding between non-genetic-relatives where a similar context exists. If this is the case, then consideration of the proximate mechanisms of social bonding becomes key to understanding how inclusive fitness selective pressure has moulded the evolution of social bonding and social behaviours in humans.

An understanding of evolutionarily typical environments and how these have shaped proximate mechanisms of behaviour is therefore important in understanding the current form of species-typical social behaviours. The following chapter will attempt to indirectly consider some fundamental aspects of evolutionarily typical environments relevant to humans. This relies heavily on defining likely evolutionarily long-term, fundamental, demographic features of *primate* groups, and those of African apes in particular.

CHAPTER SIX – THE MEDIATION OF SOCIAL BEHAVIOURS IN PRIMATES

6.1 INTRODUCTION

The previous chapter demonstrated that, in mammals, context-driven cues such as familiarity and social bonding are of key influence in mediating the expression of social behaviours between close genetic relatives. In a small number of species there is some evidence for an ability to distinguish relatives by self-referent phenotype matching, particularly between those relatives (e.g. paternal siblings) whom would not typically interact in early developmental contexts. However even in such species, familiarity regardless of actual relatedness is the over-riding influence in mediating social bonds and behaviour. In this chapter, similar findings are made of primate species.

The relevance of this chapter's enquiry into the mediation of social behaviours in primates needs clarification. Recall that 'inclusive fitness' is proposed to be best interpreted as a description of the selection pressure genes face in evolutionary environments for their social effects. In order to understand past selection pressures that have shaped current species-typical *human* behaviours, we must examine aspects of evolutionarily typical environments relevant to humans.

Evolutionary psychology posits an 'Environment of Evolutionary Adaptedness' (EEA) of a particular time period to be of primary relevance to understanding current human behavioural characteristics. The key influential period of human evolution is typically proposed to be the past two million years or so depending on what version one follows (e.g. Symons 1992, see chapter 7 for more); in all cases the focus is on the period *after* human ancestral species branched off from other African apes.

Whilst evolutionary psychologists' use of this conceptual tool (the EEA) may be an improvement on the Darwinian anthropologists' assumption (that behaviour always leads to inclusive fitness maximisation in the present - independently of evolved proximate mechanisms), the common reference to a discreet and narrowly bounded EEA is itself somewhat artificial. If one wanted to understand the *differences* in behaviour between humans and, for example, other African apes, then investigating the different unique selection pressures operating on these species and their ancestors for the past 5-7 million years or so (since divergence) would be a worthwhile approach. However, as one might expect, there are similarities in many aspects of behaviour between all African apes, (as well as deeper commonalities stemming from around 200 million years of shared mammalian ancestry). To assume that the past couple of million years is the crucial period for an understanding of fundamental aspects of current species-typical human social behaviour (and that previous evolutionary history is largely irrelevant) may be too narrow a focus. It really depends on what behaviours you are interested in analysing, and what assumptions you are already making about human uniqueness. The concept of the EEA was borrowed from the ethological attachment theorist John Bowlby. Although Bowlby also considered the past 2 million years to be influential in shaping human behaviour, his own interest was in an investigation of the mechanisms and evolution of social bonding behaviour in humans which he explicitly *linked to* similar mechanisms in other primates. Thus, rather than focusing exclusively on the past two million years of uniquely human evolutionary history, Bowlby consistently related human behaviours to historical selection pressures operating within primate environments in general (Bowlby 1982, see chapter 7).

Reviewing basic features of current primate groups which share a common evolutionary history with humans (including an investigation of other African apes) may reasonably be taken to indicate some fundamentals which have also been present in the past adaptive environments of the human species. Furthermore, this approach has the advantage of potentially outlining basic social behavioural propensities that humans have in common with other primates, independently from the theoretical framework (in this case inclusive fitness theory) referred to in the current analysis.

This chapter will first outline basic demographic influences common to many primates, and note the varieties of mating system and dispersal patterns observed in primate species. As we saw for mammals as a whole, ecological factors heavily influence demographic patterns for all primates including the African apes (section 6.3).

The chapter then gives an initial overview of the typical grouping contexts of genetic relatives (section 6.3.1) and notes the considerable incidence of groups of maternally related females in many species (section 6.3.2).

The main part of the chapter reviews evidence of the typical patterns of interaction between particular pairs of relatives. In each case, this is accompanied by a review of the evidence (sections 6.4.1 – 6.4.6) demonstrating that context-driven cues strongly mediate social bonds observed in primate species closely related to humans.

6.2 BASIC NICHE AND LIFE HISTORY VARIABLES OF OLD WORLD PRIMATES

Relative to most other mammals, primates have been studied extensively in the field, mainly due to the long standing assumption that insights gained into primate behaviour might help illuminate aspects of human behaviour (Washburn 1950). For present purposes it is necessary to draw on evidence from those primate species most closely related to humans. Although phylogenetic reconstructions are not straightforward (Hartwig 1999), there is general agreement over ancestral relatedness between primate species. The two main branches of primates, prosimians and simians (or *anthropoids*), perhaps had a common ancestor some 50-60 million years ago, and probably divided early in the Eocene period if not before. Within simian primates (the branch to which African apes belong) evidence is suggestive of a split 25-35 million years ago between the 'Old World' and 'New World' branches (see Hartwig 1999 for a recent review). Our focus in this review will be on 'Old World' primates (Order *Catarrhini*) of which the two existing sub-branches are Superfamily *Hominoidea* (Apes) and Superfamily *Cercopithecoidea*, with a single existing Family *Cercopithecidae*, comprising the subfamilies *Cercopithecinae* (e.g. baboons, macaques, vervets) and *Colobinae* (e.g. colobus, doucs, langurs).

Relevant demographic features of all Old World (*Catarrhini*) primates include the following; single births with significant birth spacing (1-2 years for most *Cercopithecidae*, 3-6 years for *Hominoidea*); extended developmental period and time to reproductive maturity (typically 3-6 years for most *Cercopithecidae*, 7+ for *Hominoidea*); and relative longevity (typically 20+ for most *Cercopithecidae*; 40+ for *Hominoidea*). These figures are consistent with highly 'K selected' species (see chapter 5.3), or what Kappeler et al. refer to as species with 'slow life histories';

> "Primate life histories are among the slowest among mammals (Harvey and Clutton-Brock 1985; Harvey, Martin and Clutton-Brock 1987; Ross 1988; Charnov and Berrigan 1993; Lee 1993; Ross 1998). Primates' birth, growth, and death rates, in particular, are substantially lower than those of other mammals after controlling for difference in body size. Specifically, primates have relatively long gestation lengths, large neonates, low reproductive rates, slow postnatal growth rates, late ages at maturity, and long life spans in comparison to other mammals (Martin and MacLarnon 1988; Charnov 1991; Harvey and Nee 1991; Lee, Majluf, and Gordon 1991; Ross 1992a; Charnov and Berrigan 1993)." (Kappeler 2003, 4-5)

In common with other mammals, ecological influences play a large part in determining both these life history variables, and the concomitant contexts of interaction between individuals.

6.3 ECOLOGICAL INFLUENCES AND DISPERSAL PATTERNS

As with other mammals (reviewed in chapter 5.3), outside the considerably important mother-offspring relationship, interactions with other genetic relatives will depend upon demographic influences such as patterns of philopatry and mating system.

Old World primate social systems are characterised by great variability both between and within species (Fuentes 1999; Yamagiwa 1999). This variability initially upset the earliest models of primate demographic structure (based on first observations) when it was discovered upon further fieldwork that subpopulations of the same species could exhibit different social systems (Fedigan & Strum 1999). For example, studies by Dolhinow (Jay 1965, Dolhinow 1972) on Hanuman langurs in north India gave the impression of a multi-male multi-female species. Independent studies in south India by Sugiyama (1965) suggested single male multi-female groups were also characteristic of the Hanuman langur. A similar flexibility of system was found to characterise different baboon populations (Fedigan & Strum 1999). As research has mounted, the only safe conclusion is that flexibility is characteristic of the majority of species, and this flexibility is reflected in the individual behavioural plasticity characteristic of primate species;

> "Even a brief examination of primate species indicates that grouping patterns, group composition, and the subsequent set of interactions within and between groups can be highly variable (Rylands 1993; Treves and Chapman 1996; Vasey 1997; Fuentes 1998; Chism, Essay 9; Freed, Essay 13; Kirkpatrick, Essay 10; Strier, Essay 11). Because these elements can be highly variable, it is likely that selection has favoured individuals who are highly adaptable in their behaviour potentials." (Fuentes 1999, 187)

Despite these variations, there is traditional classification of demographic patterns in primates, and the key patterns relevant to Old World primates are as follows;

> "Multimale, multifemale groups range greatly in size and include two or more adult males, two or more adult females and their offspring… Within this type are a number of subtypes (for example, communities, fission-fusion groups, and multilevel bands)…
> One-male, multifemale groups have one adult male and two or more adult females and offspring. Although common in cercopithecoids, this grouping pattern is less widespread than previously thought in other primate taxa…
> One-female, multimale groups… [are] very rare and only consistently reported for some callitrichid [new world] species.
> One-male, one-female groups have only one adult of each sex plus offspring. This grouping was thought to be common in primates as compared with other mammals, but recently it has been shown to be rather rare (Fuentes [2000]).
> Solitary or semi-solitary primates are those in which a female and her dependent offspring utilise a home range that overlaps with those of other female-offspring units and with multiple males. Although not truly a traditional group, these primates may be fairly social and may form sleeping associations, temporary multifemale associations, or male-female

> associations. This pattern is common in many prosimians and in one hominid [*pongo*].
>
> Although these groupings are identified by the sex of members, they do not necessarily reflect mating patterns." (Fuentes 1999, 185)

In Old World primates, only gibbon (*Hylobates*) species have traditionally been classified as living in one-male, one-female pairings (and viewed as having monogamous mating), but recent evidence has shown even this classification to be over simple (Reichard & Sommer 1997, Fuentes 2000). Additionally, as suggested by Fuentes, females of the only 'solitary' Old World primate, the orangutan (*pongo*), in fact sometimes associate with other females. Other than these notable exceptions within the *Hominoidea* branch, Old World primates typically live in social groups comprising one-male and multi-females or comprising multi-males and multi-females. Within the branch *Cercopithecidae* (*Cercopithecinae* and *Colobinae*), Andelman (1986) gives a useful summary of the structure of the *Cercopithecinae* subfamily;

> "The subfamily *Cercopithecinae* consist of four main groups: *Macaca, Papio* (including *Theropithecus*), *Cercocebus,* and *Cercopithecus* (including *Erythrocebus, Miopithecus,* and *Allenopithecus*). The basic female group structure is very similar for all Cercopithecines that have been examined, with the exception of *Papio hamadryas.* Following Wrangham (1980), Cercopithecines may be described as "female-bonded" in that females typically remain in their natal groups for life and female social interactions are characterized by pronounced dominance hierarchies and well-developed networks of grooming relationships. Males usually transfer out of their natal groups upon reaching sexual maturity. Consequently, most Cercopithecine social groups consist of a stable core of related females and their immature offspring, while the membership of adult males in such groups is more transient (*P. hamadryas* is exceptional in that females do not breed in their natal groups)…
>
> In summary, among Cercopithecines, female group size is closely related to the distribution of feeding sites. Male membership in groups, and the resulting social system, are strongly dependent on the size of female groups. In general, small female groups lead to uni-male social systems. There is a significant linear relationship between the size of the female group and the number of male members in multimale groups. At intermediate female group sizes, both social systems occur, and a variety of factors, including dispersion of females and cooperative male

> behaviour, appear to be important in determining which system prevails. The ratio of adult males to adult females in multimale groups (for which data are available) is virtually constant across species ["approximately 1:2.4"], suggesting that multimale social structures are not primarily an adaptation to high predation pressure." (Andelman 1986, 202, 216)

In primates, as with other mammals, because associations of adult females tend to be influenced by distribution of key food resources available to them, it is females which tend to be philopatric, remaining in their natal home range (with its familiar resource locations) upon maturity, whilst males tend to disperse. There are some exceptions, where males are philopatric, which will be discussed below. As Andelman's above *Cercopithecinae* summary suggests, most male polygyny is partial and relatively short term (the 'harem' arrangement of the hamadryas baboon is an exception). In the *Colobinae* subfamily, again with a few exceptions, this female philopatric pattern also holds; an brief overview is given by Boesch (1995);

> "[A]ll colobines live in social groups, but the sizes range from 4 individuals in the Mentawai leaf-monkeys to aggregations of more than 400 individuals in the golden snub-nose monkey. All live in matrilineal societies except for the three species living in the Tai' forest that live in patrilineal troops." (Boesch 1995, 796)

Pusey and Packer (1987) provide a more general overview of primate philopatry and dispersal, and demonstrate a similar pattern to that in other mammals (see chapter 5.5);

> "It is now clear that although members of one sex often remain in their natal group throughout their lives, members of the other sex usually emigrate at sexual maturity…
>
> Male-biased dispersal occurs in all the Old World monkey [*Cercopithecoidea*] species that have been well studied, except hamadryas baboons, red colobus, and possibly black colobus (*Colobus satanas*)…
>
> In most polygynous species, males provide little direct paternal care. Female reproductive success appears limited primarily by nutritional constraints, while male reproductive success seems limited more by the numbers of females they can inseminate (Trivers 1972; Bradbury and Vehrencamp 1977; Wrangham 1980). Studies of various mammals show

> that foraging efficiency is increased by familiarity with the area and the phenology of food sources and that such familiarity is best gained by remaining in the natal area (Waser and Jones 1983). As a result, females may benefit more than males from philopatry." (Pusey and Packer 1987, 250, 265)

In the *Hominoidea* (ape) branch of Old World primates, however, significantly different patterns predominate. The social system of gibbons (*Hylobates*) was briefly described above, and both sexes usually disperse from their natal range, but sons may remain if the adult male dies. The other *Hominoidea* (Orangutan, two species of Gorilla, two of Chimpanzee, Bonobo (or 'pygmy chimp') and Humans) are sometimes known as the 'great apes', and have quite different social systems. Wrangham gives an account of the potential significance of ecological influences (particularly the distribution of primary food sources) on the social organisation of the 'great ape' species;

> "For a family containing only four [since subdivided to 7] species, the social systems of the great apes are strikingly diverse. Orangutans (*Pongo pygmaeus*) are essentially solitary. Gorillas (*Gorilla gorilla*) form stable bisexual groups with rarely more than two males or six females. Chimpanzees (*Pan troglodytes*) and bonobos (or pygmy chimpanzees) (*P. Paniscus*) live in closed social networks (communities) with as many as one hundred or more individuals. Within communities the mating systems and association patterns of the two chimpanzee species differ substantially.
>
> These social variations present an attractive problem because the ecology of the four species is similar in many ways. All are confined to habitats that contain at least a small amount of tropical rain forest. They breed all year and the young travel with their mothers from birth. They sleep in nests throughout their habitats, and have no permanent sleeping sites. There are no obvious differences in their vulnerability to predation, disease, or bad weather. Their main ecological differences appear to lie in foraging patterns, and even these have striking similarities, because all species feed from rather discrete patches on easily digested food (even the gorilla: Waterman et al., 1983).
>
> Previously I have suggested that foraging patterns are primarily responsible for difference in great ape social organization. Fig. 16.1 shows that group size varies among the four species. Differences in group size are not explained by difference in population density: at any density bonobos from the largest parties and orangutans the smallest. Therefore

> food density, which presumably controls population density, is unlikely to be a strong influence on group size. Food distribution varies, however, and the nature of each species' food type and foraging style suggests that differences in average group size may be due to differences in the intensity of feeding competition." (Wrangham 1986, 352)

In respect of the key influence of food-sources on basic demographic patterns then, great apes are little different from other mammal species (see chapter 5.4). Orangutans are mainly solitary, with long-term non-coresident single-male polygyny. Females and their dependent offspring may occasionally congregate with other mother-offspring units at prime feeding sites.

Humans, bonobos, chimp species, and gorilla species are together classified as African apes, and probably had a common ancestor on the order of 5-7 million years ago. For this reason, as set out in the introduction, it may be worth considering the commonalities of all these species in any attempt to understand basic behavioural features of any one of them. Goldsmith (1999) gives a characterization of Gorillas (whose geographic distribution overlaps that of chimps), again emphasising the influence of food-sources;

> "Gorilla populations differ from one another in aspects of their ecology and behaviour. At the lowest altitudes forests are fruit-rich, and chimpanzee densities are high. In these regions gorillas are highly frugivorous, more arboreal, travel far daily distances, and, in some cases, may live in less cohesive social groups. This is similar to what we see in other African apes, especially bonobos. At the other end of the scale – at high altitudes where there are few fruit sources and no chimpanzees – gorillas are folivorous, terrestrial, travel short daily distances, and live in cohesive, stable groups. […]
>
> Mountain gorillas live in relatively stable groups of 2 to 34 members, with an average of 9.2 individuals. Although they are generally described as living in single-male, polygynous social groups, 28% of the groups have two breeding silverback males. There is much variation, but females generally transfer from their natal group and engage in secondary transfer, whereas males either remain solitary or form all-male groups. As seen in other mammals that live in single-male groups, takeovers may result in infanticide, wherein the new resident male kills offspring he has not sired.
>
> The extent to which mountain gorillas experience within group feeding competition is low due to abundant and evenly distributed food sources.

> Daily path length increases with group size, but only weakly, and competition for food between group members is low…
>
> The latest evidence from Lopé, Gabon (Tautin et al. 1992), the Ndoki Forest, Congo (Olejniczak 1996), and Bai Hokou, Central African Republic (Goldsmith 1996), suggests a mean group size of about 9.5 individuals for western lowland gorillas, similar to that of the Virunga mountain gorillas, but western lowland gorilla groups rarely exceed 16 to 18 individuals. Although most of the information on the ecology and behaviour of western lowland gorillas comes from limited observations and indirect data (due to lack of habituation), there have been no documented or suspected cases of infanticide…
>
> Although western lowland gorilla groups are frugivorous and experience within-group feeding competition, they do not live in smaller groups as predicted. How then do they reduce competition that results from feeding on sparsely distributed fruits? Western lowland gorillas increase their group spread and form smaller temporary foraging subgroups. More than five years of study at Bai Hokou has documented that gorillas form temporary subgroups that feed separately and, on occasion, sleep separately from each other (Goldsmith 1996; Remis 1997b). Although temporary subgroups form throughout the year, they occur significantly more often during the rainy season months when feeding on fruits. This behaviour is newly described for gorillas and is similar to what we see in other frugivorous African apes.” (Goldsmith 1999, 60-63)

Goldsmith’s summary clearly demonstrates the influence of ecological factors on the demographics of gorilla species. Apart from Humans, the other African ape species are of the *Pan* genus. Fruth et al. (1999) give a useful overview of their commonalities and differences;

> “Both *Pan* species [now considered 3] show many common characteristics. Their anatomy is fundamentally similar; that is, there is sexual dimorphism, males being heavier and having larger canine teeth than females (Jungers and Susman 1984; Parish, under review).
>
> Both species live in groups or communities of 20 to 120 members (Nishida 1968; Kuroda 1979; Goodall 1986). Both are diurnal, wide-ranging, and regularly form subgroups of differing number and composition, so-called parties, that range independently in a common home range. This fluid pattern is called fission-fusion social organization. Home range size varies and depends strongly on both habitat quality and community size, ranging from 6 to more than 300 km^2 (Kano 1971; Baldwin, McGrew, and Tutin 1982; Sugiyama 1984). Communities consist

> of both sexes, but females usually outnumber males (male-to-female ratio may be as much as 1:4). Males remain in their natal community, but females generally migrate to neighbouring communities, usually at sexual maturity. As a result, males know one another from childhood until death and many are closely related, whereas females are less familiar and more distantly related (Morin et al. 1994b).
>
> Depending on habitat, food patch size, and food distribution, both species travel daily distances ranging from several 100 m up to 10 km, with an average of about 3 km/day, to meet their nutritional needs (Wrangham 1997; Fruth 1995). They are omnivorous, eating ripe fruit, leaves, piths, flowers, and a small but important proportion of animal prey, such as insects or mammals…
>
> The most striking differences between the two *Pan* species occur in social organization and structure. An eye-catching difference concerns party composition (Figure 3). Chimpanzee females spend most of their time only with dependent offspring. They join males seasonally or when in estrus, whereas males range in parties year-round. Community boundaries are frequented by males, and encounters with neighbouring communities are either avoided or hostile (Goodall 1986). Bonobo females, in contrast, are typically found in mixed-sex parties, regardless of season and reproductive status. All-female parties are frequent, whereas all male parties are almost absent (Kuroda 1979). Community boundaries exist, but attractive resources in zones of overlap lead to occasional encounters between neighbouring communities. These encounters begin with agonistic displays but end up with members of both communities eating together and interacting peacefully (Kano 1992)." (Fruth et al. 1999, 64-66)

These brief summaries confirm that ecological conditions are a key influence on demographic patterns for all the African apes and that such patterns are variable within certain limits. In the following section we consider the relatedness patterns within social groups that arise from these demographics.

6.3.1 TYPICAL GROUPING CONTEXTS OF RELATIVES: OVERVIEW

Before this section jumps into analysing the typical clustering of genetic relatives brought about by these demographic arrangements, it is noteworthy to take stock of the point that clearly emerges from these accounts of the influence of ecological factors on social grouping. As we saw in chapter two, such *ecological potential must allow for social grouping* and the accompanying opportunity for interactions between individuals prior to considerations of the evolution of complex social behaviours that may be contingent upon reliable patterns of relatedness. In short, group living *per se* must be both possible and advantageous for individuals 'from the start' as Hamilton (1987) put it. Walters (1987) makes this point well;

> "I am distinguishing behaviour concentrated on relatives within groups, discussed below […] from overall levels of cooperation characterizing social groups. The issue in the latter case is to what extent particular levels of cooperation can be attributed to average relatedness of group members resulting from population structure.
>
> Some of the cooperative benefits that primates derive from group living are widespread among animals, and occur even in groups of unrelated individuals. These include benefits gained from alarm calling, improved foraging efficiency, and some forms of cooperative defense against predators. Similar behavior occurs for example in mixed species flocks of birds (Morse, 1980, Chapter 12) and in temporary flocks of wintering sanderlings (*Calidris alba*) comprised of unrelated individuals (Myers, 1983). The benefits derived from these forms of cooperation are presumably sufficiently large that high relatedness (i.e. kin selection) is not necessary for their evolution. Behavior such as cooperative defense of resources, allogrooming, and other forms of cooperative defense against predators (e.g. physical attacks on predators) are not as widespread, and their evolution may well be attributable to the levels of relatedness characteristic of primate groups." (Walters 1987, 361-362)

Within these durable groupings, we now turn to consideration of the kinds of interactions that regularly occur, their typical correlation with genetic relatedness, and the proximate mechanisms that mediate social behaviours. We start with considering the commonest demographic pattern; female-philopatric polygyny. Walters (1987) gives us an overview of how this structure shapes the typical genealogical patterns that characterise the group as a whole;

> "The best studied population structure in non-human primates is one in which groups consist of related females and their offspring, plus

> associated males (Wrangham, 1980; Moore, 1984; Pereira and Altmann, 1985; Pusey and Packer 1986). Males usually emigrate from their natal groups, and avoid mating with close kin within their natal groups even when they do not emigrate (see below). The interaction structure in this system, known as the female-bonded group system (Wrangham, 1980; Moore, 1984), thus results in the association of maternal kin. The polygynous nature of the mating structure (see below) also leads to high relatedness within groups, especially within age cohorts, but through paternal lines (J. Altmann, 1979)." (Walters 1987, 361)

Walters reminds us of what we have seen in other mammals (chapter 5.4) that mating system particularly affects paternal relatedness patterns that cut across the group as a whole (we consider this in more detail below). However, the clearest and most frequent context of interaction is between maternal relatives; mother and offspring, pre-dispersal maternal siblings of both sexes, and older maternal siblings of the philopatric sex. Gouzoules and Gouzoules (1987) discuss the predominance of this interaction between close maternally related individuals;

> "Related individuals in species of Old World monkeys that typically form multimale groups (primarily the cercopithecines, see chapters, 9, 11) are often found near and in contact with one another and may travel, feed and sleep together (e.g. pigtailed macaques; Rosenblum 1971; Rosenblum, Kaufman, and Stynes 1966; Japanese macaques; Yamada 1963; Kurland 1977; chimpanzees; Goodall 1968; Pusey 1983; yellow baboons; Altmann 1980). Mothers and their immediate offspring are particularly spatially cohesive, collateral kin (i.e., nonlineal kin such as aunts/uncles – nieces/nephews, cousins) to a lesser extent… In many species of nonhuman primates, infants and juveniles regularly interact with relatives other than their mothers (rhesus macaques; Berman 1982a, 1983a, Japanese macaques; H.Gouzoules 1980b, in prep.; yellow baboons; Altmann 1980, chapter 27; chimpanzees; Goodall 1968; gorillas; Fossey 1979; vervets; Lee 1983a). Older siblings are usually the first and most persistent individuals other than the mother to interact with infants." (Gouzoules & Gouzoules 1987, 299-303)

The extent and duration of both mother-offspring and maternal-sibling relationships will vary according to age of weaning, age of dispersal and birth spacing. Where females are philopatric, maternal sisters will tend to continue to associate as adults, perhaps still in the presence of their own mother, and in turn, their infants may encounter 'grandmothers', maternal 'aunts' and other maternal relatives in addition to the more fundamental and basic interactions with mother and maternal siblings.

As Walters (above) reminds us, a polygynous mating system can lead to a substantial number of paternal half-siblings. The duration of interaction of such paternal-siblings depends on dispersal (long for paternal sisters in a polygynous female philopatric species, such as most cercopithecines, long for paternally related brothers/males in a male philopatric species, such as chimps - though here matings are multi-male). Where typically a single male dominates matings for a few years at a time (as often occurs in gorillas) all individuals born into a group over the period of his tenure will be paternal siblings. From the individual infant's point of view, similar-aged juveniles in the group are likely to be paternal half-siblings. In other species such as chimps a number of females sexually associate with a number of males, and no one male necessarily dominates reproduction; a mother's subsequent offspring will tend to be fathered by different males, and paternal relatedness across the group will be more diffuse, although still present.

In general then, across all groups, paternal relatedness (where the mating system provides it) is reflected in age cohorts across the group and is less reliable than maternal relatedness. The latter is more localised, perhaps just constituting mother and maternal siblings (as in chimps), or perhaps other maternal relatives (in female philopatric species).

Again, as we saw for mammals in general, note that the context and degree of interaction between paternally related individuals is distinct from the context and degree of interaction between maternally related individuals. The selection pressures on social behaviours are thus asymmetrical. Whereas paternal relatedness, even where potentially significant, is variable and less reliable; interactions between maternally related individuals – particularly maternally related females – are consistently present in at least a minimal form and may be greatly extended.

6.3.2 FEMALE PHILOPATRY AND MATERNALLY RELATED FEMALES

Before looking at how 'kin recognition' is mediated in these species, a notable feature of female philopatric Old World primates is worth bearing in mind for its typical impact on the distribution of genetic relatives that the developing infant encounters. As noted above, female philopatry combined with durable groups produces a situation for such species in which maternal relatives beyond the mother-offspring unit can interact for many years, particularly female maternal relatives. These maternal relatives are sometimes referred to as 'matrilines' in the primate literature, but since this term has anthropological resonance that appears to prejudge a homology to ('descent models' of) human kinship (see e.g. above chapters 1 and 3), the current approach maintains the phrase maternal genetic relatives. Not only is there a reliable context of interaction between such maternal relatives, but these relationships have become highly socially elaborated in many species. Although this cannot always have been the case, it is worth bearing this in mind when considering why context-dependent 'kin recognition' is so ubiquitous, and thus apparently a stable mechanism in such species (reviewed below). A recent review of the frequency of interactions between such maternal relatives is given by Silk (2001) who summarises this social elaboration;

> "The importance of strong kin ties among females is most clearly documented among contemporary Old World monkeys (Gouzoules & Gouzoules 1987). In these species, maternal kinship underlies a suite of features, including female philopatry, well-differentiated relationships among females, matrilineal social networks, and stable and linear dominance hierarchies." (Silk 2001, 78)

Chapais gives a similar account;

> "[M]aternal relatedness is an important factor promoting preferential relationships in primates (Gouzoules, 1984; Walters 1987; Gouzoules and Gouzoules, 1987; Walters and Seyfarth 1987; Bernstein 1991). In female philopatric species, female kin spend their lifetimes together, producing extensive matrilineal structures that span up to four generations." (Chapais 2001, 205-206)

As well as measures such as basic proximity between maternally related individuals being high, active interactions such as grooming also accompany maternal relatedness (e.g. Kapsalis & Berman 1996, Silk & Seyfarth 1999). Walters summarises the kinds of interaction that typically accompany maternal relatedness in Old World primates;

> "That individuals behave differently towards maternal kin than toward non-kin within social groups is well documented among non-human primates. The pertinent data have been reviewed in detail in several recent papers (Gouzoules, 1984; Pereira and Altmann, 1985; Gouzoules and Gouzoules, 1986; Walters and Seyfarth, 1986). Among the presumably altruistic behaviours for which kin selection has been shown are allogrooming, alliance formation and food sharing (Silk, 1986). Other behaviors for which evidence of kin-bias exists include tolerance during feeding (co-feeding), spatial proximity, play, carrying and otherwise caring for infants, and aggression." (Walters 1987, 365)

How such social discriminations should come to reliably occur between relatives is of course dependent on the ontogeny of social bonds and behaviours implicated in the 'kin recognition' mechanisms discussed below.

6.4 THE MEDIATION OF SOCIAL BEHAVIOURS

Now that we have seen how the ecological variables and associated demographic factors influence the typical grouping contexts of genetic relatives, we can investigate the details of mechanisms mediating the expression of social 'discriminations' i.e. significant social behaviours in these primates.

6.4.1 MALE-OFFSPRING

Perhaps the most illuminating evidence is that concerning the interaction between a male and what are typically his potential offspring. In many *Catarrhini* (van Schaik 1996), infanticide by newly dominant males appears to be a common phenomenon, as it does in some other mammals (see e.g.

Goldsmith on eastern mountain gorillas above, and Waldman's brief review, in chapter 5). Hrdy (1977) was the first to suggest that this behaviour could be understood via its consequences for mating success and, due to the proximate mechanisms mediating the expression of the behaviour, that it usually accurately reflects genetic relatedness (in this case, the absence of close relatedness). Male infanticide occurs in a number of mammals in which females' fertility is suppressed by lengthy post-partum anestrus (van Schaik 1996). The benefit of the behaviour to the male is proposed to be that, in killing the dependent infant, he effectively removes the impediment to the female's fertility, and thus increases his own reproductive prospects. The context of expression of infanticidal behaviour appears to effectively limit the killing to only those individuals sired by previous males, and is circumstantially cued and 'time sensitive'. Hrdy (2000) gives a summary of primate male infanticide;

> "In many primates (34 different species, so far) infanticide is one of the more toxic effects of sexually selected competition between males. Among langur monkeys, for example, males who enter the breeding system from outside may kill unweaned infants. Over an 18-year-long study of langurs at Jodhpur, in the largest such study ever undertaken, Sommer reports that 33% of all infants die by being killed when their mothers are intercepted by males they have never mated with. […] Recent DNA evidence collected by Carolla Borries and colleagues in the first langur field study to ascertain paternity reveals that none of the victims were attacked by genetic fathers. Males who either were or might be the father (this based on both DNA evidence and behavioural observations to ascertain which males mated with the mother when she was fertile) refrain from attacking offspring of that female. At Borries's site, where males are sometimes able to remain near the mother, possible fathers actually help her to protect her infant. Since all mothers mate with multiple males, none of the protectors could be certain of paternity, yet a possibility of paternity was sufficient to alter the male's subsequent behaviour towards her offspring, presumably because past sexual history with the mother provides some sort of cue that elicits tolerant versus destructive behaviour towards her infant [note (a)]…
>
> [Note (a) reads] The best evidence for this is that even if a strange infant, temporarily kidnapped from another troop, is not attacked so long as it remains in the possession of a female who is familiar to the male." (Hrdy 2000, 78-79)

This behavioural rule operating in males which by-and-large 'tracks' genetic relatedness is thus not a 'positive power' of discrimination (see chapter 4.6). Given the potential cost to infants signalling 'the wrong' paternity, under conditions of frequent infanticide, this would be a clear case in which there would be strong selection pressure upon *concealing* genetic identity (e.g. Pagel 1997, Sherman et al. 1997, see discussion in chapter 5). Walters also gives a summary of the mediation of male-infant relationships;

> "Differential behaviour towards infants by adult males is well documented for a variety of species. Species practicing infanticide and living in one-male groups are an extreme example; adult males kill some infants and behave protectively towards others (Hrdy, 1977, 1979; Gouzoules, 1984; Struhsaker and Leland, 1986). In this case differential behaviour is highly correlated with paternity, being related to the male's period of residency in the group. Kin recognition may be based simply on period of residency or on prior sexual interaction with the mother (Gouzoules 1984).
> Differential behaviour is less pronounced in species living in multi-male groups. In baboons male association with infants is highly differentiated. Association involves spatial proximity, co-feeding, alliance formation, and in some cases reciprocation by the infant in the form of agonistic buffering (Fig. 3) (Packer, 1980; Altmann, 1980; Stein, 1981, 1984; Strum, 1983; Smuts, 1985; Whitten, 1986). Association is more closely correlated with long-term bonds between males and the mothers of the infants than with mating relationships during the period in which the infant was conceived, however (Stein, 1984; Smuts, 1985). Special relationships between infants and adult males are more subtle in macaques, but they occur in some species (Grewal, 1980b; Berenstain, Rodman and Smith, 1981). Again, however, the weak differential bonding that exists appears more closely correlated with bonds between males and females than with paternity (Berenstain, Rodman and Smith, 1981). Thus, paternal kin bias occurs in the interaction of adult male and infant baboons and macaques, but correlations for kinship behavior are not as high as for maternal kin bias. The kin recognition mechanism apparently involved, recognition through bonding with a referent individual, the mother, is imprecise." (Walters 1987, 376-377)

As well as earlier reviews such as Walters' (see also Busse 1985; Gouzoules & Gouzoules 1987) the consensus view amongst primatologists remains that interactions between a male and his possible infants are mediated via his relationship with the female caring for the infant. Paul et al. (2000) give a summary for savannah baboons that could serve for *Catarrhini* as a whole;

> “[A]lmost all researchers agree that the male’s relationship with the infant’s mother is the single most important variable for the establishment of an affiliative relationship between a male and an infant (Strum 1984; Smuts 1985)” (Paul et al. 2000, 274)

Similar evidence is available in other primate species; cues for male-infant association rely on familiarity with the mother (Davis 1984; Smuts 1985; Palombit 1999; Borries 1999; Bernstein 1999; Hrdy 2000; van Schaik 2000). With the points noted by Walters above, whether this relationship can be considered as ‘parental investment’ has been questioned. Even the unusually strong bonding between some savannah baboon males and particular infants is interpreted as ‘mating effort’ (Smuts 1985, Paul 1993) rather than ‘parental investment’, since the males subsequently stand a good chance of securing matings with the mother and often could not have fathered the infant in question;

> “Stein (1984a) looked for evidence in wild yellow baboons for a relationship between probable paternity (based on copulations around the time the mother conceived) and male relationships with infants. Probable fathers were indeed more likely than other males to develop an affiliative bond with an infant, but Smuts (1985) showed that, in olive baboons, such relationships were nearly always the result of a long-term bond between the male and the infant’s mother. Probable fathers that did not share a bond with the mother were unlikely to develop a close bond with her infant, and males that were not observed mating with the mother, but that did have a long term relationship with her, did form a close bond with the infant. These findings from the wild are consistent with results from a study of captive rhesus macaques, where true paternity was determined by analysis of genetic markers (Berenstain, Rodman, and Smith 1981). The rhesus fathers showed a slight but significant tendency to associate with their own offspring, but “the effect of paternity disappeared when maternal association with males was controlled” (p.1061). These studies of baboons and macaques cast considerable doubt on the ability of males to recognizes their own infants independent of close behavioural association.” (Gouzoules & Gouzoules 1987, 304-305)

Davis (1984) reports that association with the mother also mediates the (less significant) relationship between males and infants in chimpanzees. Recall that we saw in chapter three (section 3.2.2) that recent applications of biological theory to studies of human societies also suggests that the traditional view of the 'father role' of human males in connection with a female and offspring also should include the influence of 'mating effort', not simply 'parental investment' (Hawkes et al. 1998, 2001; Hrdy 1999, 2000; Marlowe 1999, 2001). More generally, the evidence from primates that the male's relationship with the infant is mediated through his relationship with the female is resonant with the long-standing position in anthropology over the social role of the father (see chapter 3.2.2).

6.4.2 PATERNAL SIBLINGS

The established position in primate studies is that paternal siblings do not identify each other as such nor interact preferentially;

> "The available evidence also indicate that other patrilineal relatives do not recognize themselves as kin. In pig-tailed macaques (Macaca nemestrina) and baboons (Papio cynocephalus), paternal half-siblings that were raised apart, hence were unfamiliar, did not later treat each other preferentially (Fredrickson and Sackett, 1984; Erhart *et al.*, 1997). In Barbary macaques, patrilineal kin did not avoid incestuous matings whereas matrilineal kin did (Kuester et al. 1994). Thus, although female philopatric (and for that matter male philopatric) primate groups may include several classes of paternal relatives, patrilineal kinship does not appear, on the basis of the available evidence, to translate into nepotism." (Chapais 2001, 205)

We have seen that the reliable distribution of paternal siblings (where present) will be heavily influenced by the typical mating systems occurring in *Catarrhini*. Altmann (1979) noted that paternal siblings would typically be distributed in cross-group age cohorts as a result of skew in male reproductive success. In this case the local group itself provides the fundamental context of paternal sibling interaction. However, as we saw in chapter four, because a reliable context of interaction is lacking for paternal siblings (as compared to maternal siblings), the former are a more likely candidate for self-referent phenotype matching 'recognition'. Walters' review summarises this situation;

> "Just as researchers have difficulty determining paternity within multi-male primate groups, the monkeys themselves may not be able to recognise paternal-siblings from social interaction. Intrinsic recognition mechanisms are therefore a more compelling possibility for paternal kin than for maternal kin where precise mechanisms based on social interaction are feasible. Sackett and his colleagues have examined intrinsic recognition of paternal siblings in pig-tailed macaques (*Macaca nemestrina*) in two experiments. In the first, juveniles were simultaneously exposed to two peers unknown to them, one of which was a paternal-sibling, the other an unrelated juvenile (Wu *et al.*1980). Thirteen of 16 subjects orientated more toward the related juvenile. This was originally construed as evidence of phenotype matching. However, the test situation was not a natural one in that juveniles in the wild do not have to discriminate among strangers, but among familiar group members. In the second experiment (Fredrickson and Sackett, 1984), the youngsters were tested with familiar peers as well as strangers. The subjects orientated more towards familiar animals than unfamiliar ones, regardless of paternal kinship, and did not orient more toward unfamiliar relatives that toward unfamiliar non-relatives…
>
> There is thus no evidence of precise recognition of, or kin bias towards, paternal siblings. Imprecise recognition mechanisms, and corresponding kin biases, are nevertheless possible. In both multi-male and one-male groups peers are often paternal siblings (see above). Even if paternal siblings are treated no differently from non-siblings among peers, treating peers in general differently than non-peers should result in some kin bias (J.Altmann, 1979)… If peers are treated specially as a class, then simple recognition by social context, specifically membership in an age-cohort within a group, is most likely." (Walters 1987, 378-379)

More recently, with the availability of non-invasive genetic testing, the patterns of interaction of actual paternal siblings has been analysed. Alberts (1999) investigated possible inbreeding avoidance mechanisms between paternal siblings in savannah baboons (*Papio cynocephalus*). Despite the conventional wisdom (see e.g. Chapais above), she found that;

> "The current study indicates that Baboons use social cues to avoid paternal relatives and *may use phenotypic cues as well.* The social cues,

> involving age proximity, are likely to stem from close association during the juvenile period…" (Alberts 1999, 1506, emphasis added)

Similarly, Widdig et al. (2001, 2002) found that the context of age cohorts was key for mediating affiliative interactions between paternal sisters in *Macaca mulatta* (their dataset was limited to females), but that some self-referent phenotype matching mechanism (they suggest similarity of 'personality') also appeared to supplement the discrimination. Widdig et al. (2001, 2002) also note that reciprocal play and familiarity from an early stage of development characterises age-cohort members in many primate groups. Recall that Pagel (1997) and Sherman et al. (1997) noted that negative selection upon signalling genetic relatedness would occur in those species where outcomes from signalling non-relatedness would be detrimental (see discussion in chapter 5.8). The same is the case for signalling identity in interactions between peers. Given typical mating patterns, the incidence of paternal siblings will never be wholly reliable; sometimes they are present, sometimes not. Where engaging in social interactions with peers is individually beneficial to those involved, making *any* such interaction (e.g. reciprocal play) strictly contingent on identifying actual paternal relatedness would be selected against (in both the 'initiator' and the 'target' individuals), since such relatedness may not be present much of the time. This is consistent with the findings that, although some bias towards interacting with actual paternal siblings within the age-cohort is evident, even without relatedness, familiarity with peers mediates social interactions.

In order to keep these findings suggesting a minor role for self-referent phenotype matching in perspective, note that social affiliations between paternal siblings were secondary in significance to those between maternal siblings and mother-offspring dyads (Widdig et al. 2002).

6.4.3 MATERNAL RELATIVES

As with other mammals, the interaction between female and offspring is subject to a reliable context in all primate groups. As we saw in chapter four, where this is the case, context-driven 'recognition' is likely to mediate social bonds and behaviour. Erhart et al. (1997) give a succinct summary of the mechanisms mediating discrimination between maternal relatives in primates;

> "In most nonhuman primate species, an infant is continually associated with its mother for the first part of its life and as a consequence has prolonged exposure to other maternal kin, including older and younger siblings and possibly aunts and the mother's mother. An infant's early social relationships, then, are almost all with maternal kin. Thus, selection for these maternal relationships may be the most parsimonious mechanism for explaining kin selection for savannah baboons and other nonhuman primates which share the same social organisation (Bernstein, 1991; Fedigan, 1982; Walters 1987). This conclusion is supported by errors in kin recognition of unrelated infants and close associates of the mother who receive the same social treatment as maternal relatives. We propose that, if and when nonhuman primates behave differently with members of their social group, the basis of the observed recognition may be the result of social learning and social history." (Erhart et al. 1997, 155)

The availability of maternal relatives beyond the mother-offspring unit will depend upon typical philopatry patterns (see discussion, section 6.3 above). Whilst the 'typical' patterns are clear, cases in which primate infants are adopted by individuals other than their biological mother are regularly reported (e.g. Bernstein 1991). The existence of such adoptions is interesting and will be discussed further below.

6.4.4 FEMALE-OFFSPRING

The female-offspring relationship takes place in a similar, reliable context in all *Catarrhini*. This section will look at what mediates social bonds and social behaviours *from the point of view of the adult female*. Silk states the fundamental position;

> "Apparently, even mothers must learn who their own infants are. Mother's inability to recognise their own infants at birth enables managers of captive colonies to cross-foster newborn infants (Bernstein 1991). Foster mothers routinely accept these strange infants, even if they are not the same sex or precise ages as their own infants. Female macaques are even willing to rear infants of other macaque species. (Owren et al. 1993).

> We generally assume that primates learn who their relatives are through their early experiences and associations." (Silk 2001, 74)

More recent work has further demonstrated successful inter-specific adoption (Guerra et al. 1998). The initial postnatal connection between a reproductive female and her offspring is made immediately at birth, which, as common in mammals, usually takes place in seclusion from other individuals (Swartz and Rosenblum 1981), thus typically avoiding potential ambiguity. Soon after birth, the female will learn phenotypic features of the infant (Gubernick 1981) which usually results in reliable subsequent identification. However, even at this stage, evidence from *Macaca nemestrina* suggests that a female may employ a 'rule of thumb' to identify her offspring, since if mother and infant are separated after birth, upon reunion 3-7 days later, mothers preferred the younger of two infants available, regardless of whether or not it was their own birth infant (Gubernick 1981). It is notable that the infant itself may play an active role in 'who becomes the mother', as McKenna illustrates;

> "It is also important to consider the role the infant plays in actively encouraging its own care, as Lewis and Rosenblum (1974) demonstrated a few years ago. While the precise age of the infant and its neurological maturity will affect the degree of infant manipulation, it now seems evident that the infant will control more of its own care than was previously believed. During a project in which 6-month-old Indian langurs were separated for 2 weeks from their mothers, Dolhinow (1980) was surprised to learn that despite the fact that Indian langur females are eager and frequent allomothers, the *infants* and not the adult females initiated and were responsible for their adoption by particular females. More surprising was the fact that most of the infants did not go back to their own mothers when they were reunited with them a mere 2 weeks later (see Dolhinow, 1980, and Dolhinow and De May 1983, for a discussion of adoption)." (McKenna 1987, 160)

As with other mammals (see chapter 5.7) successful fostering in many species of *Catarrhini* (e.g. Bernstein 1991) confirms that genetic relatedness *per se* is not required for the expression of maternal social behaviours (see also next section, and Harlow, reviewed in chapter 7).

Whether birth-mother or foster-mother, the typical content of social discriminations towards infants remains the same. As is discussed in the next section, the expression of social behaviours by the mother-figure towards the infant plays a major role in mediating the social bond towards her that develops in the infant. The key social behaviours expressed by the mother-figure are discussed here.

The female will normally have largely uninterrupted, continuous bodily contact with the infant for a prolonged period after birth. For example, during the first month, the proportion of time spent in direct contact may be from around 80% (Vervet, Rhesus macaque) to almost 100% (yellow baboon) of the time (data from Nicolson 1987). In the African apes, the first break in contact is typically at 4-6 months of age (Nicolson 1987 and references therein). Although contact gradually declines after the first months, the female and infant will remain in close proximity, particularly prior to weaning. This proximity may be primarily maintained by the infant after months 3-4 (savannah baboons, rhesus macaques), particularly in cold weather or rain (Nicolson 1982, 1987) or other threatening conditions.

There are significant benefits to the infant from physical 'contact' itself, such as warmth, and shelter both during waking hours and whilst asleep (together), and even provision of movement and physical stimulation (Gubernick 1981). During these periods of close contact, the female will express a range of more active social behaviours including; nursing with milk, carrying, cleaning and grooming, responding to signs of the infant's distress (e.g. in the form of vocalisations from the infant).

Another reliable context of interaction between maternal relatives, particularly mother-offspring, is co-feeding. In frugivores (the majority of *Catarrhini* with the exception of *Colobinae*), due to the patchy distribution of feeding sites (and difficulty of access for infants), individuals will usually eat in the company of close maternal relatives particularly as infants and juveniles. In a few other species, co-feeding is more elaborated, and as well as providing access to feeding sites, mothers will sometimes share food with infants. Waldman gives an overview;

> "Food-sharing among primates is relatively uncommon, although a few species collect vegetable matter to feed to their young (201). Captive

> vervet monkeys *(Cercopithecus aethiops sabaeus)* feed on prey together, usually with their close relatives (62). Primates sometimes communicate information about locations of plentiful food supplies to members of their groups (e.g. chimpanzees, *Pan troglodytes;* macaques, *Macaca sinica)*(208)." (Waldman 1988, 559)

In chimpanzees and bonobos, active food provision by mothers to offspring is common (McGrew 1996, Hohmann and Fruth 1996). Feistner and McGrew give an account of this;

> "More has been published about food-sharing in common chimpanzees than in any other species of non-human primates. In the wild, it was first reported by Goodall (1963) at the Gombe Stream reserve in Western Tanzania. Since then every long-term field study of chimpanzees that has included behavioural data has found food-sharing to occur, and, thus, it can be considered to be a 'universal' pattern within the species' repertoire (see Ghiglieri, 1984). Chimpanzees share both plant and animal foods and transfer occurs not only between mother and offspring, but also between unrelated individuals of various age and sex classes (figs. 1 and 2).
> In the first quantitative study in the wild, McGrew (1975) found that pairs of relations, e.g. mother-offspring, sib-sib, uncle-nephew, and grandmother-grandchild, accounted for 86% of banana distribution seen. Almost all of these kin-related cases involved a mother and her immature offspring, and 92% were transfers from the former to the latter." (Feistner & McGrew 1989, 25)

In summary, the levels of social behaviour and care typically directed towards infants by females are extremely high in *Catarrhini.* Swartz and Rosenblum (1981) give the following account of the level of commitment;

> "As the infant becomes active during the 1st or 2nd week of life, the mother attempts to restrain it when it tries to leave her. If the infant is successful in leaving, the mother follows the infant very closely, often with her hands hovering over the infant in a guarding fashion. She is very quick to retrieve the infant at the slightest sign of distress from the baby, or any sign of danger in the group (Bertrand, 1969; Hinde et al., 1964; Jay, 1963; Struthsaker 1971)." (Swartz & Rosenblum 1981, 423)

6.4.5 OFFSPRING-FEMALE

As with other mammals, the infant is unlikely to be particular about whom it gets care from. The distinction from most other mammals is that, being group-living, *Catarrhini* infants do potentially face a situation where individuals other than the mother are typically present from the earliest stages of development. Added to this, infants attract a great deal of attention;

> "That the infant is an effective stimulus for eliciting caretaking behaviour should be evident from the fact that in most primate species, the newborn is very attractive to members of the social group… "Aunts," nulliparous or nonpregnant females in the mother's social group, approach a newly parturient female and her infant, in attempts to touch, hold or groom the infant (Jay, 1963; Poirier, 1968; Rowell et al. 1964; Struthsaker 1971; van Lawick-Goodall, 1968)." (Swartz & Rosenblum 1981, 423)

Temporary 'allocare' ('babysitting' if you will) by individuals other than the mother is also a common feature of many *Catarrhini* (see e.g. McKenna 1987 for review). Given what we have already noted about the patterns of association and thus familiarity between maternally related individuals, in most cases, the allocarer is typically related to the mother and infant (Nicolson 1987), and may often be an older sibling of the infant. Temporary instances of allocare are different from instances of permanent adoption, but such adoptions do occasionally occur in natural conditions (arranged adoptions are not uncommon, as noted by Silk 2001, above section 6.4.4). Again, adoption is typically by individuals of close maternal relatedness (but what mediates this is again probably not genetic relatedness *per se*, but rather social bonds whose formation typically correlates with relatedness). Nicolson makes this point about adoptions and maternal relatedness;

> "When infants are orphaned, siblings often attempt to care for them; in some cases, such care may make a crucial difference to infant survival (chacma baboons: Hamilton, Busse, and Smith 1982; chimpanzees: Goodall 1983; Pusey 1983). Berman (1983b) has described a case of sibling adoption in rhesus monkeys on Cayo Santiago. By examining measures of typical patterns of mother-infant interaction, she found that the interactions between the orphaned infant and a 3-year-old nulliparous

> sister developed over a period of 2 months, through adjustments by each, into a relationship very similar to that of a mother and a similar-aged infant." (Nicolson 1987, 338)

Swartz and Rosenblum make the point that, for many *Catarrhini*, a readiness to care for 'an' infant (regardless of whether they have given birth to it) is a particularly salient feature;

> "Hence, animals who lack the biochemical composition of the newly parturient female's blood can display adequate caretaking behaviour, indicating that, although the hormonal factors may enhance interest in the new born infant, they are not necessary to the initiation of those behaviours which may normally lead to the formation of the attachment bond. Thus, DeVore (1963) has cited the case of adoption of a young female baboon by a dominant male at the death of the mother, and van Lawick-Goodall (1968) cited several cases in which orphaned chimpanzees were adopted by an older male or female sibling." (Swartz & Rosenblum 1981, 421)

Thus an infant can form a primary social bond to an individual other than the mother (even males), and such figures (often close maternal relatives) will typically be available. Given that this is the case, it follows that what mediate the formation of the social bond (from the point of view of the infant) between the infant and what would typically be its mother, are in large part the 'behaviours' that it receives from this individual, having solicited care (see also Harlow, chapter 7). In other words, what cues social bonding for the infant is not genetic relatedness *per se*, but the *very process* of receiving care and being looked after, responded to and nurtured. If this is the case then actual genetic relatedness is obviously irrelevant to the formation of the bond, and to the expression of social discriminations that accompany that bond.

Specifically, the 'context' driven formation of the bond in the infant appears to be cued by precisely those kinds of social discriminations that an infant would typically receive from its carer (as described above in the mother-offspring section). These include; being in physical contact (warmth, shelter and protection); receiving nursing; being carried (and other stimulation); being groomed and cleaned; being responded to in distress; being assisted with access to food (by transportation to food sites, and co-feeding, if not actual food provision).

6.4.6 MATERNAL SIBLING – SIBLING AND OTHER MATERNAL RELATIVES

Consistent with what we have seen for female-offspring interaction, 'recognition' between maternal relatives is agreed to be context-driven in primates;

> "There is a widespread consensus that maternal kin recognition in primates is based on a predictable social context, specifically familiarity during development (Breed and Bekoff, 1981; Bateson, 1983; Moore and Ali, 1984; Gouzoules, 1984; Gouzoules and Gouzoules, 1986)… Mechanisms based on predictable social context appear to be the rule in mammals (Bekoff, 1977, 1978; Sherman, 1980; Bekoff and Byers, 1981; Gouzoules 1984; see also chapter 10), so primates apparently are not exceptional in this regard. Such mechanisms are based on a strong correlation between interaction in a particular context and relatedness (Sherman, 1980; Holmes and Sherman, 1983). In species such as ground squirrels or canids the mechanism is straightforward; association during early development is confined to particular kin classes by the rearing situation so that particular kinds of interaction (e.g., play), bond-formation or familiarization during that time are strongly correlated with kinship. Subsequently treating others differently based on familiarity or social bonding then leads to kin bias in behavior (Bekoff, 1977, 1978; Sherman, 1980; Bekoff and Byers, 1981). The kin recognition mechanism must be more complex in non-human primates, because contact early in development is not restricted to a few close kin of a predictable class. Instead, in many species individuals are in at least occasional contact from birth with a variety of others, including the mother, maternal siblings, other maternal kin and non-relatives.
>
> One way in which kin may be recognized is through a reference individual, specifically the mother (Berman, 1978, 1982; Sherman, 1980; Holmes and Sherman, 1983; Gouzoules, 1984). Young primates learn to recognize their mothers soon after birth (McKenna, 1979b); they might then identify other kin from the way in which others interact with their mother. This mechanism requires, first of all, that primates recognize one another individually (Brown, Sanderson and Michod, 1983). There is

> abundant evidence that they do (Breed and Bekoff, 1981; Cheney and Seyfarth, 1982; Cheney, 1983; Moore and Ali, 1984), and can even retain recognition after long separation (Erwin *et al.*, 1974). The mechanism also requires certain interactions or social bonds of the mother are correlated with kinship. There is no single behavior that is directed only at close kin in most species, so the mechanism must involve the relative frequency with which the mother exchanges one or more behaviors with other group members." (Walters 1987, 374-375)

More recent evidence agrees that social bonding/'recognition' between maternal siblings is mediated via the mother in *Catarrhini* ('mediated recognition', see chapter 4). Chapais (2001) gives the following account;

> "The mother-offspring relationship appears to be at the heart of matrilineal kin recognition… This basic bond may, in turn, allow individuals to recognise other categories of uterine kin. For example, maternal siblings use familiarity based cues to recognise each other in pig-tailed macaques, as evidenced by the observation that maternal half-siblings raised apart, hence unfamiliar, did not later treat each other preferentially (Sackett and Fredrickson, 1987). The role of familiarity in maternal kin recognition is further supported by the observation that maternal kin familiar to each other avoid incestuous matings in Barbary macaques (*Macaca sylvanus*), whereas unfamiliar maternal relatives did not (Kuester et al., 1994)." (Chapais 2001, 206)

Bernstein (1991) gives a similar account;

> "The fact that matrilineal kin reared together, as well as unrelated 'adopted' animals, all treat each other preferentially, whereas patrilineal kin do not, suggests an association mechanism. Walters (1987) and MacKenzie et al., (1985) have pointed to the period of early infant association as sufficient to account for most social preferences among primates. The infant is continually associated with the mother in many primate species for the first part of its life. (It would be interesting to study kinship and behaviour correlates in taxa where this is less true, e.g. some colobines). The bond between mother and infant persists after the birth of her next infant. As a consequence, the youngest infant's first prolonged contacts are likely to be with mother and mother's other still dependent offspring. The bond between mother and child (especially female offspring) may be prolonged and enduring so that infants are likely

> to find older siblings also in proximity. Moreover, mother's mother may also still be in association, and mother's female siblings may be in proximity as well." (Bernstein 1991, 19)

Both accounts illustrate that contextually driven, mediated 'recognition' does not guarantee social bonding on the basis of genetic relatedness *per se*.

Maternal siblings exhibit the typical social discriminations of mutual grooming and solidarity to counter aggression from (as well as hand out aggression towards) other individuals within the group (see Silk above). Additionally, as suggested in the discussion of allocare and fostering above, a maternal sibling may also express nurturing behaviours towards a younger sibling. Gubernick notes that;

> "[L]ong-term genealogical information necessary to determine kinship networks is available for only a few species, and those are primates. Such information is available for the chimpanzee, *Pan troglodytes* (van Lawick-Goodall, 1967, 1968, 1971), rhesus monkey, *Macaca mulatta* (Kornford, 1963a,b; Sade, 1965), and Japanese macaque, *M. fuscata* (e.g. Itani, 1959; Kawamura, 1958; Yamada, 1963). In such matrifocal groups an infant usually remains associated with its mother after the birth of the next infant. In each of the above species it is usually the mother's kin, especially previous daughters, that help care for and protect the infant (see also Poirier, 1968, for Nilgiri langurs, *Presbytis johnii*)." (Gubernick 1981, 269-270)

Given the close interaction between maternal relatives, it is unsurprising that when infants are orphaned, adoptions that may follow (see examples above) are often by maternal relatives;

> "Maternal kin have been observed to care for orphaned infants in several species (e.g. Marsden and Vessey, 1968; Hasegawa and Hiraiwa, 1980; Hamilton, Busse and Smith, 1982). Care in such cases consists of carrying, grooming, sleeping with, and defending the infant… With respect to altruistic interaction, the relationship between an orphaned juvenile female yellow baboon and her sister was identical to that between her peers and their mothers (Walters, 1981, in preparation)." (Walters 1987, 372-373)

Gouzoules and Gouzoules (1987) also discuss sibling interactions and 'adoptions' in the African apes;

> "Older siblings are usually the first and most persistent individuals other than the mother to interact with infants. For instance, Fossey (1979) reported that siblings were more consistently near infant gorillas than any other class of individuals except mothers, and that this proximity was maintained throughout the first 3 years of an infant's life. In chimpanzees, older siblings interact a great deal with infants, touching, grooming, protecting, playing, and even briefly "kidnapping" them (Goodall 1968). Most interestingly, several cases of adoption of infants by older siblings were also recorded at Gombe. Orphaned infants without siblings were not adopted by other chimpanzees in the community." (Gouzoules & Gouzoules 1987, 303)

Given the tendency of chimpanzee communities to be male philopatric, without the availability of maternal siblings, an infant would have few if any other maternal kin nearby. Marsden (2000) gives further examples of adoptions by older siblings in chimps, including by brothers.

In sum, it is notable that relationships between maternal siblings, who are typically separated in age by at least two years in most species of *Catarrhini*, and at least four years in African Apes, are characterised by aspects of the care and nurture which typically accompany the mother-offspring relationship.

6.5 SUMMARY

In the first part of the chapter we found that ecological factors heavily influence demographic patterns in primate species, just as they do for other mammals. This in turn influences the typical contexts of interaction of genetic relatives.

The evidence has demonstrated that social bonds and social behaviours in primates are mediated by social context. Whilst we have seen tentative suggestions that some positive powers of discrimination may occur between paternal siblings, even here, context-based cues also operate to mediate social interactions and usually outweigh positive powers. For all other social bonds that would typically characterise genetic relatives, context-based cues are in operation.

Central to these social bonds is the relationship between what are typically mother and offspring. The basic features of this relationship both in humans and in other primates have been studied by attachment theorists, as the next chapter will review.

CHAPTER SEVEN – ATTACHMENT

7.1 INTRODUCTION

Earlier chapters have reviewed the basic biological theory of the evolution of social behaviours (particularly chapters 2 and 4). It has been suggested that the sociobiological applications to anthropological data have misrepresented biological theory, and that a focus on the typical evolutionary context of an organism's behaviour is a necessary part of any application of inclusive fitness theory to understanding current behaviour. In other words, inclusive fitness theory should not be understood to make deterministic predictions about the specific *outcomes* of organisms' behaviours in any given instance, only as a description of the general statistical outcomes (the criterion) necessary for *the long term evolution* of social behaviours within a species over evolutionary time scales. For an analysis of behavioural characteristics of a given species, theory simply emphasises that this potential selection pressure will result in proximate behavioural mechanisms governing social behaviour and social bonding, which by-and-large (in typical environments) have met the inclusive fitness 'criterion'.

The evidence in mammals confirms that social discriminations are largely mediated by familiarity and social bonding between individuals. In turn, the development of these social bonds overwhelmingly relies on *circumstantial* cues, rather than genetic relatedness *per se*. This has also been confirmed for primates (this chapter will add a little more detail on the primate mechanisms).

This finding about the importance of circumstantial cues also clarifies the first issue posed by integration of biological theory with ethnographic data on human social behaviour: Basic biological theory (inclusive fitness theory) *does not predict* that an individual's key social bonds (and social behaviour) will necessarily be with genetic relatives *per se*.

A further issue is whether we can give an account of mechanisms of social bonding which is both compatible with inclusive fitness theory and for which we can find evidence in humans. Towards this end, the previous chapter built upon the general evidence derived from the review of social bonding in mammals, and provided us with some insights into specific mechanisms that operate in *Catarrhini* primates. The current chapter continues by looking at the general findings of the ethological attachment theorists who have explicitly conceived of human social bonding instincts within a primate-wide framework, and thus provide a useful bridge for the current approach.

The further relevance of reviewing attachment studies is for their description of the empirical findings on *mechanisms of social bonding in humans*. In the second part of this chapter we will be attempting to define key characteristics of these processes of social bonding which can then be carried forward in order to check against the ethnographic data and summaries (in chapter 8).

Some of the assumptions accompanying early attachment theory's descriptions of the norms of social bonding (e.g. gender roles and number of attachment figures) were limited by a culturally narrow empirical base. Some of the debates and developments in this area are discussed both in this chapter (sections 7.5.4, 7.5.5) and in chapter nine.

7.2 CONFIRMING THAT SOCIAL BONDING MEDIATES SOCIAL BEHAVIOUR IN HUMANS

As noted in chapter two, social behaviour can take many forms, and is hard to quantify. In general 'social behaviour' as we defined it in chapter two is an accompanying characteristic of social bonds, particularly primary social bonds that typically form between close genetic relatives (such as mother and offspring) as was discussed in chapter five (5.10). In the primate and human case, I also make this simplifying assumption, supported by many different perspectives; that social bonds are accompanied by social behaviours (as defined in chapter 2), in order not to have to include a formal analysis of the presence of 'social behaviour'.

Anthropology also typically makes this assumption in its analysis of human social behaviour. Although the 'content' of social relationships is sometimes described, it is usually treated generally as 'amity', 'altruism' or 'generosity' (Fortes 1969) or 'code for conduct' (Schneider 1968, 1984) and is suggested to accompany the patterns of social bonding which are often the subject under focus. Fortes' work on the 'axiom of amity' that accompanies social bonds (which he refers to as 'kinship') demonstrates this most clearly. He speaks of;

> "[A] general principle of kinship morality that is rooted in the familial domain and is assumed everywhere to be axiomatically binding. This is the rule of prescriptive altruism which I have referred to as the principle of kinship amity and which Hiatt calls the ethic of generosity…
> Though the structural connotation which the notion of kinship carries varies widely, the central value premise associated with it is uniform. Kinship predicates the axiom of amity, the prescriptive altruism exhibited in the ethic of generosity… kinsfolk are expected to be loving, just and generous to one another and not to demand strictly equivalent returns from one another." (Fortes 1969, 232, 237)

Although making the behaviours typically accompanying 'kinship' fairly explicit, Fortes doesn't claim to be the first to make this suggestion. He notes that others have referred to "kinship solidarity" (Phillpotts 1913) and expectations of "immediate support and protection" (Schapera 1950). Particularly interesting for its relevance to the current chapter, Fortes quotes a lengthy passage from Young and Willmott's (1957) study of social relationships which nowhere mentions 'kinship' and instead talks of 'attachment';

> "Though they [mother and daughter] both derive benefit from the relationship, it is far more than a mere arrangement for mutual convenience. The attachment between them is supported by a powerful moral code… in most of these families… duty and affection seem to co-exist, and indeed, reinforce each other." (Young and Willmott 1957, 161, quoted in Fortes 1969)

Fortes also states that "It is conceivable – and I for one would accept – that the axiom of amity reflects biological and psychological parameters of human social existence." However, as noted in chapter one, too often biological referents for social bonding by 'kinship' theorists were made whilst not explicitly examined, and genealogy and social bonding conflated (Schneider 1984). Schneider suggests that, were we to remove the genealogical assumption, 'prescriptive altruism' might be a starting point for analysis of what is usually referred to as 'kinship';

> "If kinship were defined in some other terms – for example, as the axiom of prescriptive altruism – then genealogy would become structurally and logically secondary. It might still be quite important, but it could not have the logical priority it has now. We would be bound first to establish that the axiom of prescriptive altruism obtained and second to correlate different factors, such as genealogy, with the defining criterion… [in some societies, it is argued] kinship is defined in terms of both landholding and blood relationship. For other societies it is argued that kinship is defined in terms of some special code for conduct such as the axiom of prescriptive altruism." (Schneider 1984, 130)

Schneider's (1968) analysis of *American Kinship* suggested that "code for conduct" is an integral part of the kinship concept within American culture, albeit also defined genealogically. Although Schneider (1980) was not keen to see the concepts he derived from American culture uncritically universalised through alignment with Fortes' 'axiom of amity,' other ethnographers have suggested 'diffuse enduring solidarity' might characterise social bonds in other cultures (including Witherspoon (1975), one of Schneider's students). Many anthropologists have referred to the social behaviours and/or expectation of behaviour which accompany social bonds and relationships. These may be expressed as "rights and privileges, duties and obligations" (e.g. Barnes 1955, Scheffler and Lounsbury 1971, Pitt-Rivers 1973) or even "attachment and obligation" (e.g. McKinley 2001). Sahlins' (1976), whilst critical of sociobiology, suggests that kinship systems "are true models of and for social action… manifested in behaviours of altruism…" (Sahlins 1976, 25). As well as this undercurrent amongst traditional kinship theory, many contemporary anthropologists explicitly discuss 'kinship' as social bonds (and 'attachment') and link this to social behaviour (see chapters 8 and 9).

Social psychologists also make the connection between social bonding and social behaviour. For example, in the long-standing debate over how best to characterise the relationship between feelings of empathy and acts of altruism (see e.g. Batson & Shaw 1991 and commentary), Zahn-Waxler suggests that altruistic behaviour and 'cooperative awareness' begins with primary social bonds and attachments;

> "Research by Batson and his colleagues has focussed on conditions that determine young adults' potential willingness to help unfamiliar others in highly controlled, constrained, structured environments. This may limit analyses of empathy to those aspects that are more planful, reasoned, and goal orientated. This nondevelopmental approach bypasses the affective origins of empathy and the question of how humans come to be caring, committed, and responsible individuals, as well as self-serving. Moreover, it ignores the family unit which provides, in the view of many, the main context for emergent empathy and altruism… The origins of altruism are likely to evolve, as Batson and Shaw suggest, in the context of an attachment relationship in which parent and child forge bonds that create, in their terms, a "we-feeling." Many observational studies of mother-infant interaction during the first year of life document the complex interplay of sharing and exchange of emotions, as well as cooperation and turn-taking in social interactions (e.g. Trevarthen, 1977). These early forms of "cooperative awareness" between caregiver and child begin to create a world of shared meaning, empathic understanding and appropriate linking of one's own emotions with those of others that then generalize beyond the parent-child dyad." (Zahn-Waxler 1991, 155-156)

Relevant to the current research, Korchmaros and Kenny (2001) have argued that 'emotional closeness' may mediate "the effect of genetic relatedness on altruism". They not only link these emotional bonds to the performance of social behaviours, (supporting the current simplifying assumption) but advance them as 'proximate mechanisms' in an inclusive fitness theory framework. This is very welcome (note that they employ the non-anthropological meaning of 'kin' in the below);

> "[R]esearch has shown that people are systematically more willing to act altruistically toward nonkin whom they are close to and care about than towards kin, even kin of high degrees of genetic relatedness. For example, Essock-Vitale and McGuire (1985) showed that although women's willingness to assist other people increased as genetic relatedness increased among kin, women tended to be more willing to aid friends than kin…
>
> The present study is an attempt to integrate the findings of evolutionary and social psychology. Inclusive fitness theory (Hamilton, 1964), an

> evolutionary theory, explains social behaviours in terms of ultimate causes and is useful at predicting the overall patterns of these behaviours (e.g. willingness to act altruistically as genetic relatedness increases). However, inclusive fitness theory does not address the underlying psychological mechanisms that cause the overall patterns of behaviour to occur (Cunningham, Druen, & Barbee, 1997). Social psychological theorists, in contrast, focus on psychological mechanisms, the proximate causes of behaviour. Merging evolutionary and social psychology enables simultaneous examination of ultimate and proximate causes of social behaviours and enables a more complete understanding of those behaviours…
>
> The present study, conducted from the perspective of inclusive fitness theory (Hamilton, 1964), provides a new and more comprehensive interpretation of altruistic behaviour than previously premised by inclusive fitness theorists. People are not simply calculators of costs and benefits acting in response to information specifying amount of shared genes and reproductive value. There is another component: emotional closeness. Individuals form relationships and spend time together. Consequently, they become interdependent, feel concern for each other, and are willing to act altruistically toward one another." (Korchmaros and Kenny 2001, 262-264)

A similar perspective on the place of emotional ties and empathy in mediating social behaviours, taking into account inclusive fitness theory, has also been suggested for other primates (Preston & de Waal 2002). In brief, the simplifying assumption that the current analysis makes – that 'social bonding' mediates social behaviours – is agreed upon by both animal behaviourists and human social psychologists. In turn, anthropological discussions of the social bonds traditionally referred to as 'kinship' also link these to social behaviour.

7.3 RELEVANCE OF INFANT SOCIAL BONDING INSTINCTS

Are findings about the social bonding instincts of infants relevant to a general understanding of how inclusive fitness theory applies to humans? If we accept the above argument that mechanisms of social bonding are a key area shaped by selection pressure upon inclusive fitness, then the question can be reduced to issues about the relationship of infantile social bonding to those bonds occurring at later stages of development. On the one hand is the potential enduring importance of those actual bonds formed in infancy, and on the other is whether the mediation of social bonds in later life bears resemblance to mechanisms operating in infancy.

In chapter two, it was argued that what we discover about the kinds of factors that mediate the expression of social behaviour between (typically) the closest genetic relatives (in particular whether actual genetic relatedness a necessary condition) should also be generalisable to other social bonds.

If the mechanisms of social bonding which typically operate between an infant and its mother are of an indirect nature, and are cued and mediated by certain conditions, and if such social bonds formed in infancy and childhood tend to be (and particularly would have been in evolutionary environments) significant throughout the lifespan, then they are of relevance to the investigation. Supporting arguments for this perspective come from both from the findings of attachment studies, reviewed below (section 7.5), and from ethnographic evidence (chapter 8).

7.4 ATTACHMENT THEORY'S COMPATIBILITY WITH EVOLUTIONARY BIOLOGY

7.4.1 INTRODUCTION

At this stage of the thesis, we are mainly interested in the empirical findings of attachment research, since we are looking for details of social bonding mechanisms that operate in humans. However, to support the wider claim that an understanding of infants' social bonding instincts is directly related to biological theory of social behaviour, it is notable that Bowlby saw his work on human bonding as fitting into the context of primate sociability in general (see below).

In the following sections we will see that Bowlby not only formulated attachment theory in reference to the evolutionary biology of social behaviour, but in particular, to inclusive fitness theory. He also interpreted the biological theory to require focus on evolutionarily typical contexts, and particularly emphasised that the relationship between female and offspring as the most fundamental regular social interaction for all mammals.

7.4.2 ANIMAL BEHAVIOUR AND ETHOLOGY

From the start, Bowlby, the key architect of attachment theory, was interested in other species (Ainsworth and Bowlby 1991) and acknowledged help from a number of animal ethologists in preparation of his work (including Huxley, Lorenz, Tinbergen and Hinde). He states that "The theoretical schema elaborated stems partly from psychoanalysis and partly from ethology"(Bowlby 1982, xvii).

> "Recognising, as Darwin the founding father of ethology himself did, that the behavioural repertoire of each species is as unique as are its morphological and physiological characteristics, ethologists have sought to understand behavioural equipment by reference to the contribution it makes to the survival of members of the species and their kin in the natural habitat of that species. To their following of this principle so consistently are largely due the distinctive and distinguished contributions that they have made to an understanding of behaviour. A main thesis of this book is that the same principle must be followed equally consistently if we are to understand the instinctive behaviour of man." (Bowlby 1982, 55)

Recall Hamilton's own early interpretations of how selection pressure on social behaviour (to meet the inclusive fitness criterion) would be visible in the ontogeny of animal behaviours. Hamilton (1964) drew heavily on the work of ethologists when illustrating behaviours that he felt demonstrated this selection pressure (see Hamilton's references to Tinbergen's ethological work on typical mechanisms of parent-offspring bonding in birds, in chapter 2.2.4). These mechanisms of bonding, and the behaviours accompanying them are clearly central to what Hamilton himself believed inclusive fitness theory to be relevant to. Conversely, Bowlby recognised the basic currency of inclusive fitness theory within evolutionary biology.

7.4.3 BOWLBY'S SUPPORT OF INCLUSIVE FITNESS THEORY

Bowlby's first theoretical treatment of attachment behaviour (Bowlby 1958), although drawing heavily upon the data and theoretical perspective of ethology, did not discuss the theoretical aspects of the *evolution* of social behaviours *per se*, and pre-dated Hamilton's work. His first volume of the larger work *Attachment* (Bowlby 1969) also essentially pre-dated the growing currency of inclusive fitness theory. However, such was the link between inclusive fitness theory and the social bonding behaviours that Bowlby's work focused on, that he felt compelled to produce a revision (Bowlby 1982) of the earlier volume incorporating this shift;

> "The principle reason for preparing a revised edition of this work is that during the past fifteen years there have been major developments in the thinking of biologists studying the social behaviour of species other than man. These developments have necessitated significant changes in a few places…" (Bowlby 1982, xvi)

> "During the 1960s a revolution took place in the biological study of social behaviour. Until then there had been much confusion about the identity of the biological unit that is adapted… the belief has arisen that that unit of adaptation is the social group itself… The basic concept of the genetical theory of natural selection is that the unit central to the whole process is the individual gene… The genetical theory of natural selection is clearly described by Williams in his *Adaptation and Natural Selection* (1966). In it he demonstrates how the many forms of social behaviour observed in animals can be understood in terms of gene selection, making it unnecessary for a theory of group selection to account for them. A recent more popular account is given by Dawkins in his *Selfish Gene* (1976)…" (Bowlby 1982, 57)

Williams (1966) had debated the relative parsimony of 'group selection' and 'gene selection' accounts of the evolution of certain behaviours, and was one of the first to discuss Hamilton's work (which itself had drawn on some of Williams' earlier work). The following passage leaves no doubt that Bowlby also felt that behaviours typically accompanying the parent-offspring relationship are a key example of the sort of social behaviours that inclusive fitness theory is relevant to;

> “Some instinctive behaviour is so structured that it commonly achieves food-intake and good nutrition, and as such may appear to fulfil a function of value only to an individual… there is other instinctive behaviour that is so structured that it commonly fulfils a function of obvious benefit to some other individual though of no benefit to the performer. An example is the caregiving behaviour of parents towards their young. Other examples include the helpful behaviour of individuals towards kin other than offspring, notably siblings, nephews, nieces, and sometimes cousins. In every case the behaviour is readily intelligible in terms of gene survival. Offspring carry half the genes of each parent; and, on average, siblings have half their genes in common.” (Bowlby 1982, 132)

7.4.4 BOWLBY’S FOCUS ON THE EVOLUTIONARILY TYPICAL CONTEXT OF BEHAVIOURS

Being predominantly interested in species-typical instinctive behaviours, it is perhaps little wonder that Bowlby avoided the problem of overlooking proximate behaviours that had characterised Darwinian anthropologists’ interpretations of evolutionary biology (see particularly Kitcher’s critique, reviewed in chapter 3). Indeed, Bowlby’s emphasis on the importance of considering behaviours in their evolutionarily typical context (his ‘environment of evolutionary adaptedness’ or EEA) was later to be a key component in evolutionary psychology’s conceptual critique of Darwinian anthropology (see chapter 3.5 and chapter 6.1). This section briefly reviews this aspect of Bowlby’s approach;

> “Although the survival of the genes an individual is carrying must always be the ultimate criterion when biological adaptedness is being evaluated, it is often convenient to consider the adaptedness of any part of an organism’s equipment in terms of some proximate outcome.” (Bowlby 1982, 56)

> “For most species of animal the natural habitat not only is of limited variation but also changes only slowly. As a result each species is living today in an environment little different from the one in which its behavioural equipment was evolved… For man this is not so… This leads to the conclusion that the environment in terms of which the adaptedness of man’s instinctive equipment must be considered is the one man has

> inhabited for two million years until changes of the past few thousand years led to the extraordinary variety of habitats that he occupies today… This means that man's primeval environment is, almost certainly, also his environment of evolutionary adaptedness." (Bowlby 1982, 59)

Although Bowlby is the source of evolutionary psychology's concept of the EEA, the interpretation of 'which is the critical period' of past evolution for current species-typical behaviours is quite different. Symons (1992), a prominent proponent of the evolutionary psychology approach, gives the definition; "[T]he human environment of evolutionary adaptedness (EEA) – i.e., the Pleistocene environment in which the overwhelming majority of human evolution occurred…" (Symons 1992, 143). The Pleistocene is generally understood to refer to the period lasting from around 1.5-2m years ago to the end of the last ice age (about 10,000 years ago). Evolutionary psychology thus typically uses the EEA concept to refer to a posited environment unique to *recent* human ancestors, long after those ancestors began to inhabit separate environments from those currently occupied by the other African Apes. Unsurprisingly, this focus is usually accompanied by a modelling of the evolution of 'unique to human' behaviours (see fuller discussion in chapter 6.1). Ironically, Bowlby himself was keenly interested in what he felt to be primate-wide behaviours, and thus draws heavily on cross-species analysis and comparisons in his description of the infant's social bonding instincts;

> "Just as Darwin found it impossible to understand the structure of an orchid flower until he knew what insects flourished and visited it in its environment of adaptedness, so, it is held, it is impossible to understand man's instinctive behaviour until we know something of the environment in which it evolved. For a picture of this we need to turn to anthropological studies of human communities living in the least modified of human environments, to archaeological studies of early man, and to field studies of the higher primates… Whereas some social groups are reasonably stable, others change in size and composition. But whether the larger group is stable or not, the tie between a mother and her children is always present and virtually unchanging… [I]t seems clear that man's primeval way of living can fruitfully be compared with the ways of living of the other large ground-dwelling species of higher primate. Differences between man and sub-human species there certainly are; but for the

> purposes of this book, it is argued, their similarities are equally important, and perhaps more so than their differences." (Bowlby 1982, 61-62)

7.4.5 BOWLBY ON PRIMATE FUNDAMENTALS

The last chapter dealt in depth with the basic demographic conditions faced by current *Catarrhini* primate species, and posited that many of those fundamentals are likely to have been essentially the same for the ancestors of modern humans even though current demographic conditions for many human populations are clearly very different. The aim in this section is not to spend more time on considering primate fundamentals *per se*, rather to illustrate the compatibility of this approach with that of Bowlby, and to support the claim that much of what mediates social bonding in humans resembles that in other primates. The data reviewed by Bowlby below focus on *Catarrhini* primates, and look at the same fundamentals analysed by the current approach (see chapter 6);

> "Reviewing the reports of Sade (1965) for rhesus monkeys and of Goodall (1965) for chimpanzees, Washburn, Jay, and Lancaster (1965) remark that these kinship sub-groups are 'determined by the necessarily close association of mother with newborn infant, which is extended through time and generations and allowed to ramify into close associations between siblings'; and they express their belief 'that this pattern of enduring social relations between a mother and her offspring will be found in other species of primates'… [T]hat the child's tie to his mother is the human version of behaviour seen commonly in many other species of animal seems now indisputable; and it is in this perspective that the nature of the tie is examined… [W]hatever behaviour is found in non-human primates we can be confident is likely to be truly homologous with what obtains in man." (Bowlby 1982, 183)

Bowlby also notes that this fundamental relationship between a female and her offspring, can (particularly when combined with female philopatry in species such as *Macaca mulatta*) result in several generations of maternal relatives typically being in close proximity;

> "[I]t has become evident not only that in each band there are stable sub-groups, composed of several adult animals of both sexes and a number of juveniles and infants all of which remain in proximity to one another, but that all the members of such a sub-group may be the children and grandchildren of a single elderly female." (Bowlby 1982, 187)

Notice the resonance of Bowlby's analysis with the conditions outlined in the previous chapter. Bowlby goes on to note that a key feature of African apes (here chimpanzees) is the lifelong influence of the social ties and loyalties formed in infancy. This has relevance for the current investigation, since it supports the idea that the bonds formed in infancy (for both humans and other primates) typically have an enduring influence in the social partners and social behaviours an individual engages with well into adulthood. This adds support to the current claim that studying mechanisms of infant social bonding is of key relevance to understanding life-long patterns of social bonding;

> "Goodall (1975) reports that in most of the cases for which evidence is available close relationships between a mother and her offspring, and also between siblings, persist throughout the life-cycle… [I]n a study at the Gombe Stream Reserve, Pusey (1978) observed that each of four juvenile females whose mothers were still alive spent at least four-fifths of their time in the company of her mother; and only after their first oestrus did they begin to spend less time with mother and more with adult males. Similarly, up to the time of reaching puberty, males were still spending at least half of their time with mother; and each of them continued to meet his mother occasionally up to the time of her death. Throughout these years of increasing independence the initiative for departure and return seems to lie with the young animal; no signs of a mother discouraging or rejecting one of her offspring have been observed." (Bowlby 1982, 190-191)

7.5 PART TWO – ATTACHMENT MECHANISMS

7.5.1 INTRODUCTION

The following sections will introduce the broad workings of the attachment process and its basic features. A full appreciation of these is inextricably linked to evolutionary pressures and typical demographic fundamentals of primates as discussed in previous sections and chapters. We will see that the infant's attachment to a carer tracks mainly the latter's responsiveness to the infant's elicitations for various forms of care and nurture, rather than tracking relatedness. This will confirm that, at least for this most primary of social bonds, genetic relatedness *per se* is irrelevant to their proximate development. On the contrary, the evidence is that it is the actual process of provision of care and responsiveness to the infant's needs which cues the formation of an attachment bond within the infant.

This aspect of the process has a strong resonance with anthropological descriptions of 'kinship bonds' being mediated through *'the doing of'* nurturant behaviours, rather than existing by virtue of *'being'* a blood relatives *per se* (see Schneider 1984, in chapter 1, and chapters 8 and 9).

7.5.2 OVERVIEW OF THE ATTACHMENT PROCESS

Geiger (1996) gives a useful summary of the mutual behaviours that must occur in order for the child to form a bond with a carer;

> "Attachment theorists now suggest that infants are biologically predisposed to emit signals such as tracking visually, crying, smiling, vocalising, clinging, etc., to elicit nurturance and proximity not only to their mother, but also to their father or any other caregiver (Ainsworth, Bell & Stayton, 1974; Lamb, 1978b). Consistent and prompt responding to infants' signals leads to infants' perception of adults as concerned, predictable, and reliable, and to the formation of secure attachment. Mothers, fathers and other caregivers, by their different styles of responding, create a different set of expectations and an array of attachment relationships of various qualities and flavours (Bretherton, 1985; Bridges, Connell & Belsky, 1988; Stroufe, 1988)." (Geiger 1996, 6)

Lamb also provides a similar overview of the process of the infant's elicitations, a social partner's responsiveness, and the infant's perception of this;

> "Perhaps the most useful formulation is that of the ethological attachment theorists (Ainsworth, 1973; Bowlby, 1969; Lamb & Easterbrooks, 1981; Lamb & Gilbride, 1985; Lamb, Thompson, Gardner & Charnov, 1985)

> who propose that infants are biologically predisposed to emit signals (e.g. cries and smiles) to which adults are biologically predisposed to respond. When adults consistently respond promptly and appropriately to infant signals, infants come to perceive them as predictable and reliable." (Lamb 1997, 105)

Bowlby (1982), quotes Ainsworth (1963) to emphasise that the process of the infant's seeking social interactions and then forming social bonds is *initiated by the infant itself* rather than being imposed from outside, and that this eliciting behaviour is very much 'instinctive';

> "One feature of attachment behaviour that struck me especially was the extent to which the infant himself takes the initiative in seeking interaction. At least from two months of age onwards, and increasingly through the first year of life, these infants were not so much passive and recipient as active in seeking interaction." (Ainsworth 1963, cited in Bowlby 1982, 203)

Notice that this is resonant with McKenna's (1987) discussion of *Catarrhini* primates (chapter 6.4.4). In addition to an infant's tendency to seek interaction, Bowlby gives some further details (followed up in section 7.5.6 below) of specific conditions under which an infant is particularly likely to elicit a response and attention from a carer;

> "Many conditions activate attachment behaviour. The simplest perhaps is sheer distance from the mother… Other conditions well known to activate attachment behaviour and to influence the form it takes and the intensity with which it is exhibited fall under three main heads:
> 1- Condition of the child: fatigue; hunger; pain; cold; ill health
> 2- Whereabouts and behaviour of mother: mother absent; mother departing; mother discouraging of proximity
> 3- Other environmental conditions: occurrence of alarming events; rebuffs by other adults or children." (Bowlby 1982, 258-259)

Note that Bowlby's use of the term "mother" is a shorthand, and that (as he confirms below) relatedness *per se* is not a factor in the formation of attachments.

7.5.3 CONFIRMING THAT 'RELATEDNESS' IS UNNECESSARY

The last chapter (chapter 6) confirmed that, for primates, primary social bonds can form on the basis of nurturant treatment of the infant regardless of actual relatedness. Bowlby was highly influenced by Harlow's work with rhesus macaques (*Macaca mulatta*), and it is thus worth noting Harlow's position on adoptions and the formation of attachments in primates. As Ainsworth later noted for humans, and McKenna for other primates (see previous section), Harlow emphasises the impetus given to the formation of primary social relationships by the infant itself via its own active elicitations;

> "We have observed the behavior of two multiparous rhesus monkeys (299 and 385) whose own infants were removed on the day of birth. After a separation interval of 9 and 4 months, respectively, these females were given the opportunity to adopt infant monkeys.
>
> The procedure in the case of female 385 was to separate a 78-day-old infant from its real mother by inserting a Plexiglass screen between them and to give the infant access to the cage of the prospective adopting mother. After the infant's real mother was removed from the room, the infant immediately ran to and contacted female 385. Overtly normal patterns of motherhood appeared and were maintained until the infant was forcibly removed 3 months later.
>
> A different procedure was used with female 299. A 38-day-old infant was placed in an open-field test situation and the female subsequently introduced. During the first few minutes after the female entered, the infant orientated and moved toward her several times but could make no contact because she [the adult] was seated on a shelf 3 feet above the floor. The infant, noticeably disturbed, alternately cried and screeched, while the female frequently looked at the infant. After this brief delay, the female suddenly dropped to the floor, picked up the infant, and held it for the remainder of the session and during transport back to her cage. She was not observed to release it for 3 days. Again, entirely normal mother-infant relationships were established and maintained until the pair were separated by the experimenter some months later.
>
> In both cases, the behaviour of the infants was similar in that they actively sought out the female." (Harlow 1986 [1963], 168-169)

Harlow goes on to note that an infant deprived of any mother for several weeks from birth subsequently failed to initiate interaction in the presence of adults, and, although contacted and groomed intermittently by an adult female, never responded, and social bonds failed to develop. Harlow interpreted this as further demonstrating the importance of the infant's active participation in the interaction. Overall it is clear that Harlow believed that relatedness is unnecessary in the basic process of formation of both the infant-to-carer attachment, and the bond between the caregiver and infant.

Although Bowlby's conceptual framework makes frequent reference to the 'mother' (or the 'parents'), Bowlby repeatedly confirmed that in terms of the workings of the bonding mechanisms, the figure(s) who perform the caregiving role, and to whom the infant forms attachment bonds, need not be the biological mother;

> "Although throughout this book the text refers usually to 'mother' and not to 'mother-figure', it is to be understood that in every case reference is to the person who mothers a child and to whom he becomes attached. For most children, of course, that person is also his natural mother." (Bowlby 1982, 29)

> "Observations such as these and many others make it abundantly clear that, although it is usual for a child's natural mother to be his principle attachment-figure, the role can be effectively taken by others. Such evidence as we have is that, provided a mother-substitute behaves in a mothering way towards a child, he will treat her as any other child would treat his natural mother. Just what comprises a 'mothering way' of treating a child will be discussed in the next section. Briefly, it appears to be engaging in lively social interaction with him, and responding readily to his signals and approaches." (Bowlby 1982, 306)

This passage clearly demonstrates that Bowlby understands social bonds forming as the result of a process, and 'social interaction' itself is central to that process, and thus relatedness is incidental. This emphasis on the importance of 'interaction' is further confirmed by Bowlby's discussion of the results of Ainsworth's Baltimore research;

> "The results of that study (Ainsworth and others, 1978) show clearly that two variables are significantly related to development of attachment behaviour: (i) sensitivity of mother in responding to her baby's signals,

> and (ii) the amount and nature of interaction between mother and baby. The mothers whose infants are most securely attached to them are mothers who respond to their babies' signals promptly and appropriately, and who engage in much social interchange with them - to the delight of each party." (Bowlby 1982, 315-316)

7.5.4 MULTIPLE TARGETS AND THE CONTEXT OF BONDING

A further consideration, rarely dwelt upon by early attachment theorists, is that the wider social context within which an infant encounters the 'social interaction' or 'interchange' so central to bonding will depend a great deal on the typical living arrangements of the culture in which an infant develops. It may be that a limited sample contributed to Bowlby's interpretation of the potential for patterns of social interactions and diversity of possible attachment figures (See Mead below). Anthropologists are (especially post-Schneider), of course, more interested in varieties of living arrangements, and the subtleties of patterns of social bonding.

As well as emphasising that the attachment figure need not be the 'natural mother', Bowlby discusses the flexibility surrounding the potential targets of attachment bonds in some further detail;

> "In the discussion so far it has been implied that a child directs his behaviour towards one particular figure, referred to either as his mother-figure or even simply as his mother. This usage, which for the sake of brevity is unavoidable, has nonetheless given rise on occasion to misunderstanding [Bowlby inserts a note which reads:] For example, it has sometimes been alleged that I have expressed the view that mothering should always be provided by a child's natural mother and also that mothering 'cannot be safely distributed among several figures' (Mead, 1962). No such views have been expressed by me." (Bowlby 1982, 303)

Bowlby certainly accepted that the infant can potentially form multiple social bonds;

> "Of fifty-eight Scottish infants studied by Schaffer and Emerson (1964a), 17 (29 per cent) are reported to have been directing attachment behaviour

> towards more than one figure almost from the time they started showing it to anyone. After another four months not only had half the children more than one attachment-figure but a number of them had as many as five or more different attachment-figures. By the time these children had reached eighteen months of age, those who still restricted their attachment behaviour to only one figure had fallen to 3 per cent of the sample; which means that for a child of 18 months to have only one attachment figure is quite exceptional. Ainsworth's findings for the Ganda study show a comparable state of affairs: all but a tiny minority were showing multiple attachments by nine or ten months of age." (Bowlby 1982, 304)

The question of whether an infant is likely to have access to single or multiple carers is inseparable from the question of typical living arrangements of the culture in which the child develops. As mentioned, Bowlby scarcely discusses the issue of the wider social context within which any such 'social interactions' might typically take place. However, he does briefly mention that, (at least in the cultures within his samples), the context of 'the household' appears to be a constant 'containing set' for the formation of an infant's attachments (see section 7.5.6 below).

In this section, we briefly look at living arrangements for the effect they have on the infant's forming of multiple attachments. Tronick et al. (1985) studied the communal organisation of many aspects of infant care amongst the Efe of the Ituri forest of Zaire. The Efe have different living arrangements from those in many Euro-American Cultures;

> "The Efe live in virilocal bands, with 6-50 residents, and although some bands have relatively stable membership with a consistent set of families, there is a great deal of flexibility of membership. The Efe in this study area are traditionally classified as hunters and gatherers… The Efe are semi-nomadic. The pattern of movement over a year partly reflects seasonal variation in the availability of forest and cultivated foods and affects Efe work patterns and social organization. For approximately 7 months of the year they live in encampments near a Walese village, often on the perimeter of the village fields… For the remaining 5 months of the year, the Efe move deeper into the forest to camps 1-3 days walk from the villages… The life of the Efe is that of continuous social contact. There are few solitary tasks or settings…" (Tronick et al. 1985, 302-307)

Tronick et al. go on to describe how childcare is typically organised in this culture;

> "This pattern of assistance, caring for the infant while the mother engages in other tasks, continues as the infant gets older. These observations indicate that, over the first half year of life and particularly over the first few weeks, whether in camp or out, the infant is almost always held in close bodily contact and seldom if ever put down or left alone. Access to a breast is virtually constant and upon demand. However, the mother although present may not be – indeed (with respect to holding and carrying) tends not to be – the sole caregiver of the infant. Rather, infants have multiple caretakers whose interactions with them are typically playful and sensitive. For example, in one 1-hour session, a 4-month-old was transferred nine times among six different people. To summarise, Efe infants during the first six months of life and to a lesser extent throughout the following year and a half experience multiple caretaking, including nursing by women other than the mother." (Tronick et al. 1985, 305)

Endicott also provides an account of shared responsibility for child rearing in a Malaysian society whose living arrangements are quite different from the isolated discrete households of Western societies. She describes the flexibility of living arrangements thus;

> "The Batek De' dialect group in the Lebir River area consists of about 84 people. Usually from 5 to 8 nuclear families camp together, each family in a separate lean-to shelter. The average camp population was 34 persons… camps, as physical entities and groups, generally last a week to 10 days before people move to find new food or trade resources… Families erect lean-tos at random locations, rarely more than a few yards from each other. These shelters are open on three sides, thus exposing the activities of camp members to the full view of everyone else in camp…
> A fact of life for Batek children is that the groups around them constantly change. With each move, the composition of a camp group may shift dramatically… Correlated with this freedom to leave social groupings in Batek society is the ease with which individuals can attach themselves to others. Individuals can choose who they want to work and camp with, and they select their own marriage partners… In cases of divorce, very young children, especially nursing infants, usually remain with the mother, but older children may decide for themselves with which parent they will live. Children may alternate between the parents, live with older siblings,

> or even live with stepparents who are no longer married to their biological parent." (Endicott 1992, 282-283)

As for other aspects of child rearing, Endicott points out that for such fundamentals as the provision of food, the families do not operate as isolated caregiving units;

> "The flexibility of social groupings is facilitated by the campwide sharing network that entitles all people in a camp to food. All food – whether vegetable or meat and whether procured by women or men – is shared, unless the quantities are so small as to be considered enough for only one or two people. Parents often give their children plates of food to deliver to other families in camp. This sharing occurs even when each family has procured similar food through their own labors. In addition to ensuring that all people have direct access to foods that they may not be able to procure themselves… the sharing network facilitates childcare: raising children does not create overbearing burdens on individual caregivers; through the sharing network, the entire camp absorbs responsibility for feeding children." (Endicott 1992, 283-284)

These descriptions demonstrate that the typical organisation of childcare in the Euro-American societies usually sampled by attachment theorists is not necessarily generalisable cross-culturally. Strictly speaking, Bowlby's position is not that multiple attachments cannot form. His interpretation is rather that there will typically be one figure of particular importance, rather than all social ties being equivalent;

> "[I]t is a mistake to suppose that a young child diffuses his attachment over many figures in such a way that he gets along with no strong attachment to anyone, and consequently without missing any particular person when that person is away. On the contrary, both the older evidence and that more recently available (Rutter, 1981, Ainsworth, 1982) supports a hypothesis advanced in an earlier paper (Bowlby, 1958), namely that there is a strong bias for attachment behaviour to become directed mainly towards one particular person. In support of that view attention was drawn to the way in which young children in a residential nursery tend, when given any opportunity, to latch themselves on to a particular nurse." (Bowlby 1982, 308-309)

Overall, the widely accepted position regarding the openness of the identity and multiplicity of caregivers is summarised by Archer and Lloyd (2002), who also discuss the impact of the work of Schaffer & Emerson (1964), Geiger (1996) and others;

> "Geiger's research provides a clear answer to the question as to whether an infant's mother is a privileged object of attachment, and establishes that an infant's response is not determined by the sex of its primary caregiver. In the work of Schaffer and Emerson, we noted that, in addition to forming multiple attachments, a small proportion of infants became primarily attached to their fathers. The clear conclusion is that the object of initial attachment need not be the natural mother or even female." (Archer & Lloyd 2002, 173-174)

Archer and Lloyd's summary, noting Geiger's demonstration that a male can serve as the primary attachment figure, reminds us of adoptions by older siblings (even males) in chimps (chapter 6.4.6). Before we move on, it is worth noting the evidence for sibling caretaking in humans. Whilst this may be less common in Euro-American societies, it is common in other societies, and often features in ethnographic accounts (for an early example, see Mead 1928, on Samoan society). A sample (HRAF) survey by Barry and Paxson (1971) suggested that female children are the principle companions or caretakers of infants in 16.7% of societies, and this figure extends to 53.9% for caretaking of charges who are in early childhood. McKenna (1987) also discusses the lack of acknowledgement in traditional attachment accounts of the realities of childcare in many non-Western societies;

> "[T]he cross-cultural data on multiple care-giving within what have been called "polymatric" societies, as compared with societies in which there is a single care giving figure, so-called "monomatric" societies, indicate that there is a need to better evaluate what constitutes infant care among humans. More attention needs to be focused upon what differentiates the kind of care that is given and at what age and under what amounts of supervision young care givers (or any care givers) are assuming responsibility for their infant charges (see Weisner and Gallimore, 1977); Whiting and Whiting, 1975; Super, 1981).
>
> Weisner and Gallimore (1977) have called attention to the fact that in most societies around the world siblings spend, if not more time caring

> for children than mothers do, at least significant amounts of time with them. Unfortunately, much research on child development tends to ignore these important contributions. Super (1981) argues persuasively that a "firm" enough empirical basis of quantitative, well-focused data as devoid of narrow presuppositions as possible is desperately needed. His excellent review demonstrates that the nature of supplemental care, its form and function, is but one of the many sets of problems in need of serious rethinking among infant researchers." (McKenna 1987, 174-175)

In a later chapter (chapter 9) I argue that a key research tradition which is currently extending our understanding of the formation of social bonds and attachments is that of ethnographic study, which, unlike many accounts of attachment, benefits from being informed by non-Western societies. The descriptions, in this and the previous section, of the broad variety of figures who are ready to provide significant care giving to the infant and child demonstrate that there is *no necessary determinacy* for the biological mother *per se to* be the caregiving figure, and that healthy care giving bonds can readily form in the absence of biological relatedness. This is in agreement with the findings on primates and other mammals that have emerged from previous chapters.

7.5.5 BASIC FEATURES OF ATTACHMENT BEHAVIOUR EXTEND INTO ADULTHOOD

At the beginning of the chapter (section 7.3) we noted the relevance of an analysis of basic features of attachment behaviour commonly occurring in infants and children to an understanding of social bonding behaviour in general; both to the extent that early bonds are maintained into adulthood; and to the extent that adult social bonding has similar features. As noted above, one of the limitations of much attachment theory is that, despite its broad grounding in ethology and its subject matter being universals of human behaviour, many of the studies are limited to Western society. This orientation is noticeable in discussions of attachments in adulthood, the social context of which perhaps differs more between cultures than does the social context of infancy (indeed Bowlby viewed the latter as having common features across all primate species). Because attachment theorists' discussions of adult attachments are typically informed by Euro-American arrangements, concepts and culture (though see Weiss 1991, below), this is an area where ethnographic reports can provide valuable additional insights (see chapter 8).

It is clear that attachment theorists conceive of attachment mechanisms in childhood to also be relevant to attachment and social bonds in adulthood. Bowlby suggested that attachment behaviours "characterize human beings from the cradle to the grave" (Bowlby, 1979, 129, cf. Rothbard & Shaver 1991). The following passage illustrates that Bowlby (albeit talking about Euro-American culture) felt that later social bonds are based on the same dispositions that operate in childhood;

> "During adolescence a measure of attachment behaviour is commonly directed not only towards persons outside the family but also towards groups and institutions other that the family. A school or college, a work group, a religious group or a political group can come to constitute for many people a subordinate attachment-'figure', and for some people a principle attachment-'figure'. In such cases, it seems probable, the development of attachment to a group is mediated, at least initially, by attachment to a person holding a prominent position within that group… That attachment behaviour in adult life is a straightforward continuation of attachment behaviour in childhood is shown by the circumstances that lead an adult's attachment behaviour to become more readily excited. In sickness and calamity, adults often become demanding of others; in conditions of sudden danger or disaster a person will almost certainly seek proximity to another known and trusted person. In such circumstances an increase of attachment behaviour is recognised by all as natural." (Bowlby 1982, 207-208)

Berman and Sperling (1994) suggest that caregiving and care-seeking are inextricably linked in adult attachments (see also Carnelley et al. 1996, Carpenter 2001);

> "Within the domain of adult attachment, we suggest that the theory should combine the attachment system (originally characterized by care-seeking or proximity-seeking behaviors) with a nurturance system characterized by caregiving behaviours… In contrast to the perspective that attachment and caregiving are independent but related behavioural systems, we believe that the caregiving system is an integral component and direct outgrowth of the attachment system. This is particularly true in

> the realm of adult attachment, although it may be applicable to attachment across the life span. {[here they note] It may be that even in parent-infant attachment, attachment and caregiving are part of the same nurturance system. The caregiving behaviors of the parent may also serve to foster the parent's attachment to his or her child (Weiss, 1988). For example, proximity to one's child gives a parent the experience of "felt security," even though safety of the *parent* is not relevant. Conversely, in the experience of parenting, one is confronted with intense anxiety when one's child is inaccessible, whereas proximity is reassuring even in the face of real danger…}
>
> Clearly, functioning adult marital or sexual relationships require reciprocity and easy interchange between caregiving and attachment roles (Ainsworth, 1985). The same can be said of parent-child relationships when the children are grown. It is rare that parents do not accept help, support, or nurturance from an adult child, even while they remain an attachment figure to their child.
>
> [O]ur personal and clinical experiences suggest that the emotional experiences that are bound up in attachment are exactly those that are bound up in caregiving. The fear of danger or threat triggers caregiving responses, just as it triggers attachment responses." (Berman & Sperling 1994, 9)

This interplay of reciprocated caregiving, nurture and bonding plays a significant role then not just in infant attachments, but also in adult attachments, and has been well documented by anthropologists (e.g. Witherspoon 1975, Marshall 1977, Schneider 1984, Stafford 2000, see chapter 8). Ainsworth (1989) discusses social bonds beyond the parent-child and marital ones, albeit here apparently in reference to Euro-American culture, and agrees that proximity-seeking and caregiving may both be components of some such bonds;

> "Friendship can connote a wide range of dyadic relationships, including relationships with acquaintances with whom one has occasional pleasant interaction, relationships with congenial companions with whom one spends quite a great deal of time in activities of mutual concern or interest, and close intimate relationships with one or a few particularly valued persons whose company one seeks intermittently. It seems likely that some of these relationships are sufficiently close and enduring to be characterized as affectional bonds, in which the partner is felt to be a

> uniquely valued person, not interchangeable with anyone else who might play a similar role.
> Weiss (1982) suggested that such bonds often exist between army buddies and that these bonds may be identified as attachments. Indeed, there seem to be both attachment and caregiving components in such bonds. The partners seek proximity to each other; they give care and protection to each other; separation or threat of separation occasions anxiety, and loss would certainly cause grief." (Ainsworth 1989, 714)

Weiss (1991) notes that many of these analyses (including his own) should be considered to be potentially culturally-specific. He also confirms that, despite these problems, there is enough evidence to conclude that adult attachment bonds are developments of the behaviours that operate in childhood;

> "That particular relationships should be attachments – that, for example, the pair [romantic/marital] bond should quite regularly be an attachment relationship – may be true only in societies whose social arrangements are like ours. In societies of different social arrangements the adult arrangements that regularly display properties of childhood attachment might be different…
> It appears that aside from choice of attachment figure, relationship to attachment figure, and nature of triggering threat, the properties of childhood attachment and adult attachment are the same. They are, in general, alike in the feelings associated with their arousal. They are also alike motivationally, in their ability to command attention and energy under conditions of threat. Only in their perceptual aspects are they different. So, they differ in the image of the attachment figure and the target of the triggering threat. This is consistent with the idea that we are dealing with the same emotional system, but one whose perceptual elements have been modified.
> Loss of the attachment figure, in attachment relationships of adult life as in childhood attachment, produces grief. Separation protest as a component of grief in adults is similar to the separation protest of childhood attachment in behavioural expression. In each case a syndrome can be observed that includes calling and crying, determined and sometimes frantic search, persisting perceptual recall of the lost figure, restlessness, and eventual despair. The indefinite persistence of grief in adult attachments is also similar to the persistence of childhood distress on loss of the attachment figure." (Weiss 1991, 86-69)

In sum, although this chapter focuses on social bonding processes relevant to infants and children, these commentators agree that the same basic mechanisms are at work in forming and maintaining social bonds throughout the lifespan.

7.5.6 SOCIAL ORGANISATION, EXPOSURE AND FAMILIARITY

Although not analysing them in any detail, Bowlby did realise that the typical living arrangements of a culture influence infants' social exposure and thus potential attachment bonds;

> "It is evident that whom a child selects as his principle attachment-figure, and to how many other figures he becomes attached, turn in large part on who cares for him and on the composition of the household in which he is living. As a matter of empirical fact there can be no doubt that in virtually every culture the people in question are most likely to be his natural mother, father, older siblings, and perhaps grandparents, and that it is from amongst these figures that a child is most likely to select both his principle attachment-figure and his subsidiary figures." (Bowlby 1982, 305)

Confirming the potential importance of the household, he later adds;

> "For both the Ganda and the Scottish infants the commonest subsidiary figures to be reported were father and older siblings. Others included a grandparent or other persons staying in the house, and occasionally a neighbour… Inevitably, for each child both the number and the identity of these additional figures change over time. Schaffer and Emerson record how, for a particular child, there might be a sudden increase in the number of figures and later perhaps a decrease. As a rule, though not always, such changes clearly reflected who happened to be available in the household at the time." (Bowlby 1982, 307)

In those cultures where 'households' are discrete and are the predominant or exclusive context of an infant's social interactions, then both primary and secondary attachments would (following the theory) be expected to be limited to this context. Most of Bowlby's data is derived from such cultures, but is he right to suggest that in virtually every culture individuals develop in a 'household' comprised purely of a nuclear family (mother, father, siblings and perhaps grandparents)? The examples from Tronick et al. and Endicott (see section 7.5.4) suggest this is not always the case. These variables are of relevance to ethnographic and cross-cultural investigations of social bonding norms, and will be looked at further in the following chapter.

The importance of 'household composition' demonstrates the influence that *familiarity* plays in the formation of attachment. In summarising the conditions under which an infant comes to form attachments to certain particular individuals, Bowlby notes that;

> "In determining this course of development, at least four processes are likely to be at work:
> A- an in-built bias towards looking at certain patterns in preference to others and at things that move;
> B- exposure learning, by which the familiar comes to be distinguished from the strange;
> C- an in-built bias to approach the familiar (and later to withdraw from the strange);
> D- feedback of results, by which a behavioural sequence is augmented when it is followed by certain results and diminished when it is followed by others." (Bowlby 1982, 273)

The condition of familiarity via an association with the primary attachment figure also influences the formation of secondary attachments (this resembles 'mediated recognition' as described for interactions typically accompanying maternal relatedness in female philopatric primates, e.g. Walters 1987, chapter 6.4.6);

> "[A]fter their third birthday most children become increasingly able in a strange place to feel secure with subordinate attachment figures, for example, a relative or a school teacher. Even so, such feeling of security is conditional. First, the subordinate figures must be familiar people, preferably those whom the child has got to know whilst in the company of his mother." (Bowlby 1982, 205)

7.5.7 SOCIAL INTERACTION AND NURTURE

I have tried to demonstrate that a consideration of the social/living arrangements the infant develops within will define the breadth of exposure to, and variety of, everyday social interactions. Within the primary living context, in which potential caregivers are *familiar* figures, the more specific behaviours mediating attachments, as we saw above (section 7.5.2), are broadly described as '*social interaction*' (Bowlby 1982, 306) or 'social interchange' (Bowlby 1982, 316) and more specifically *responsiveness* to the elicitations of the infant.

These conditions give us a good basic foundation with which to approach the ethnographic accounts of human social bonding (chapter 8). More detailed specification of what mediates social bonds is not always readily discussed in the attachment literature. However, the accounts reviewed above make it clear that an important component of 'care' involves responsiveness to infant elicitations. Recall that Bowlby suggested certain conditions of the infant are particularly likely to activate elicitation, including "fatigue, hunger, pain, cold and ill-health" (see full quote above, 7.5.2). Whilst pain and ill-heath would occur on an occasional basis, cold, fatigue and hunger are likely to be more regular states. Responsiveness to the infant's elicitations when it is hungry can only be met by the provision of food. Potential cold and fatigue are relieved by what attachment theorists often refer to as 'contact comfort', and a safe place in which to sleep. I briefly discuss both 'contact comfort' and feeding here.

Prior to Harlow's work with primates, the dominant model of what mediates an infant's bond to its carer was that the infant forms a 'secondary drive' for the carer due to its experience and association of the carer fulfilling its 'primary drive' of feeding. This model was known as Secondary Drive theory (Hull 1943);

> "The position commonly held by psychologists and sociologists is quite clear: the basic motives are, for the most part, the primary drives – particularly hunger, thirst, elimination, pain, and sex – and all other motives, including love or affection, are derived or secondary drives. The mother is associated with the reduction of the primary drives –

> particularly hunger, thirst and pain – and through learning, affection or love is derived." (Harlow 1986 [1958], 102)

In a later review, Harlow describes the essential elements of his findings. Note the importance of warmth as a component of 'contact comfort';

> "The cloth surrogate was originally designed to test the relative importance of body contact in contrast to activities of the breast, and the results were clear beyond all expectation. Body contact was of overpowering importance by any measure taken, even contact time… In one experiment, we heated the surface of a wire surrogate and let four infant macaques choose between this heated mother and a room-temperature cloth mother. The neonatal monkeys clearly preferred the former. With increasing age this difference decreased, and at approximately 15 days the preference reversed. In a second experiment, we used two differently coloured cloth surrogates and heated one and not the other. The infants preferred the hot surrogate, but frequently contacted the room-temperature surrogate for considerable periods of time… It is clear that warmth is a variable of major importance, particularly in the neonate, and we hazard the guess that elevated temperature is a variable of importance in the operation of all the affectional systems…" (Harlow 1986 [1970], 121-132)

Geiger's (1996) research on humans, in particular the ability for males to become infants' primary attachment figures, supports this position;

> "Hull's drive reduction hypothesis (1943), that mothers acquire the value of a secondary reinforcer by satisfying their infant's hunger drive, has been disconfirmed. By contrast, Harlow's contrary hypothesis (1961) has been confirmed. This hypothesis assumed that it was not the actual feeding but the circumstances surrounding the feeding, namely, the warmth and comfort provided by the caregiver that were at the origin of the infant-mother bond." (Geiger 1996, 96)

These findings about 'contact comfort' and particularly warmth, as well as the 'security from danger' aspect of attachment are compatible with the findings of primatologists (reviewed by Nicolson, see chapter 6.4.4) that infant and carer are in almost continuous physical contact for the first weeks (*Cercopithecidae*) or months (*Hominoidea*). Bowlby's review of primate social interaction included discussion of the universality of maintaining close physical contact between infant and carer. A related universal arrangement relevant to relieving the condition of 'fatigue' is sleeping in physical contact with the carer observed in all primates. Bowlby notes that this pattern of behaviour endures at night throughout juvenility, even when daytime contact reduces;

> "At birth or soon after, all primate infants, bar the human, cling to their mothers. Throughout early childhood they are either in direct physical contact with mother or only a few feet or yards from her. Mother reciprocates and keeps the infant close to her. As the young grow older the proportion of the day when they are in direct contact with mother diminishes and the distance of their excursions increases; but they continue to sleep with her at night and to rush to her side at the least alarm." (Bowlby 1982, 184)

Bowlby summarises relevant observations for specific *Catarrhini*. For macaques;

> "Although during their second year infants spend most of their daytime hours in sight of but out of physical contact with mother, most of them nonetheless are in actual contact with her for a substantial fraction of their day – usually from 10 to 20 percent of it – and for the whole night." (Bowlby 1982, 186)

For baboons;

> "From six months onwards play with peers increases and absorbs a large part of the young baboon's time and energy. Nevertheless, until about twelve months it remains fairly close to the mother and always sleeps with her… By the end of its second year an infant's mother is likely to have a new baby but the youngster continues to spend time near her and frequently sleeps with her at night." (Bowlby 1982, 188-189)

For chimps;

> "The next eighteen months, until the age of three years, see increasing activity away from the mother and play with companions, and the young chimpanzee is out of physical contact with the mother for as much as 75 to 90 per cent of the day. Nevertheless it continues to be transported by

> her, jockey-fashion unless she is moving fast, and it still sleeps with her.” (Bowlby 1982, 190)

Bowlby also notes that similar sleeping patterns occur in gorillas (Bowlby 1982, 192). It thus seems likely that co-sleeping arrangements - either in direct physical contact or sharing a sleeping-nest - are a regular ‘interaction’ context that serve as a ‘response’ to infant needs and elicitations. Beyond straightforward familiarity, social interaction and care, sleeping arrangements and physical comfort are thus a potential candidate of significance in our consideration of what specific kinds of interaction contexts mediate human social bonding.

Harlow’s research demonstrated that, at least in infant macaques, the importance of feeding *per se* had been overstated by secondary drive theorists. Nevertheless, that infants’ elicitations to potential caregivers are heavily motivated by hunger is firmly established within attachment theory. Ainsworth & Bowlby (1991) illustrate this in discussing the results of Ainsworth’s ‘strange situation’ and longitudinal home visit (Baltimore) research;

> “Highlights of the findings are as follows. Mothers who fairly consistently responded promptly to infant crying early-on had infants who by the end of the first year cried relatively little and were securely attached. Indeed, mothers who were sensitively and appropriately responsive to infant signals in general, including feeding signals, fostered secure infant-mother attachment.” (Ainsworth & Bowlby 1991, 338, see refs in original)

Bowlby (1982) also mentions the part that hunger plays in motivating elicitations in other primates;

> “Some other conditions that lead attachment behaviour to be shown, or shown more intensely, are reported in the accounts of infants raised by human foster-parents. Rowell reports that when her young baboon was hungry ‘he was insistent in maintaining contact and screamed continually if left.’” (Bowlby 1982, 196)

It was noted in chapter six (6.4.4) that for frugivorous primates, in addition to the access to feeding sites provided by a carer, feeding for infants and juveniles usually occurs in the company of others (who are typically relatives). Further, we saw that for chimps, the carer may share food with the infant or juvenile, and thus the period of dependency on the carer for food is extended (weaning is at around 5-6 years in chimps). As Harlow's work was with macaques (weaning around 1-2 years) where active sharing of food by the carer is rare, it may be that his findings are unrepresentative of the significance of food provision (of both milk and later food stuffs) in humans (and chimps). In fact, although initially downplaying the place of hunger and feeding in the formation of attachments (Harlow 1958, see above quotes) in later reviews, Harlow too was clear that food and feeding are of importance in macaques;

> "Although the original surrogate papers (Harlow, 1958; Harlow & Zimmermann, 1959) were written as if activities associated with the breast, particularly nursing, were of no importance, this is doubtless incorrect. There were no statistically significant differences in time spent by the babies on the lactating versus nonlactating cloth surrogate and on the lactating versus nonlactating wire surrogates, but the fact is that there were consistent preferences for both the cloth and the wire lactating surrogates and that these tendencies held for both the situations of time on surrogate and frequency of surrogate preference when the infant was exposed to a fear stimulus… [T]he infants showed a consistent preference for the lactating surrogate when contact comfort was held constant." (Harlow 1986 [1970], 122-124)

This demonstrates that, whilst the research was able to show the primacy of warmth and contact comfort in mediating attachment (particularly for newborns), the artificial dichotomisation of the surrogate into <warmth or food provision> (i.e. *being cold* versus *being hungry*) may have under-emphasised the importance of feeding under normal circumstances. Lamb (1985) gives an apt summary of the outcomes of Harlow's research;

> "Taken together, Harlow's experimental research and the nonexperimental studies of children in institutions led developmentalists to conclude that: (1) "contact comfort" (in addition to feeding) was important; (2) the secondary drive theory interpretation of early relationship formation was inadequate…" (Lamb et al. 1985, 12)

In short, for humans, both contact comfort and warmth as well as the provision of food and co-feeding are significant candidates for factors mediating the infant's attachment to its caregivers. As mentioned above, these are just some of the forms of 'responsiveness' and interaction likely to mediate an infant's bond to its carer and the caregivers' bonds to the infant; other less visible or tangible forms of nurture are surely also important, including play, responsiveness, recognition, communication and 'talking', as well as other kinds of physical and mental stimulation. Given that deconstructing 'social interaction' and 'responsiveness' is not necessarily straightforward, it is understandable that Bowlby often used these broad terms in defining what kinds of behaviour mediate the infant's attachments. Similarly, as we will see in the next chapter, ethnographic accounts, although sometimes focusing on food provision or sleeping arrangements, usually employ the broad concepts of 'nurture' and 'caring' to describe the behaviours that mediate social bonds.

CHAPTER EIGHT – ETHNOGRAPHIC COMPATIBILITY

8.1 INTRODUCTION

The previous chapters have reviewed the theoretical position in biology and noted its compatibility with the findings of attachment theory (chapter 7). Having found much evidence that various processes of interaction, responsiveness and nurture mediate the social bonding of the infant to caregivers and vice-versa, and that these continue to mediate bonds throughout the lifespan, we are now in a position to look for support (or disagreement) for this perspective in the ethnographic literature.

This chapter will start with a brief review of the development of attention paid to cultural ideas concerning the basis of social bonding. It will be seen that prior to the questions raised about the study of 'kinship' by Schneider and others from the 1960s onwards (see chapters 1 and 9), anthropology paid very little attention to the notion that social bonds were connected to anything other than consanguinal relatedness (or its local extensions). The social bonding associated with provision of and sharing of food was one important exception, particularly in the work of Richards, who tried to bring together social and biological perspectives (see section 8.3), but this was largely ignored by descriptions of 'kinship' till more recently. Although questioning the means by which 'kinship bonds' form, few of these early accounts questioned the fundamental role of 'procreative ties' in social bonding (Schneider, 1984, see chapter 1). From the 1950s onwards, reports on kinship patterns in the New Guinea Highlands added some momentum to the older suggestion that living together (co-residence) underlies social bonding, and eventually contributed to the general shift away from a genealogical approach (see section 8.5).

By the 1970s ethnographic reports started to emerge which paid greater attention to these non-genealogical, processual aspects of 'kinship' and social bonding. At the same time these reports included a significant focus on the formation of social bonds in *infants and children*, in contrast to anthropology's historical attention to ties of 'kinship' between adults - and usually adult males (see also chapter 1.3.2 and chapter 9.2). The main emphasis of the current chapter will be in reviewing a sample of such ethnographic reports, and assessing their compatibility with the ideas discussed in the last chapters. To review *all* relevant ethnographies would be a major task beyond the means of the current research, and therefore there are doubtless important ethnographies which have been overlooked. This review nevertheless demonstrates that very often in contemporary ethnographies, there is a strong focus on processes mediating social bonding, and sometimes explicit use of notions of 'attachment'.

The final section of the chapter will summarise these findings. Chapter nine will be a discussion of the main ideas and findings of the thesis as a whole.

8.2 EARLY DISCUSSIONS OF PROCESSES MEDIATING KINSHIP BONDING

Perhaps a good place to start is with Robertson Smith's (1889) compiled *Lectures on the Religion of the Semites*. Though his main focus was on clanship and 'kinsmen' rather than social bonding *per se*, he noted the significance of commensality (eating together) in forming social bonds, and noted that this is a means by which bonds of kinship can be acquired, rather than simply being 'an affair of birth';

> "The ethical significance which thus appertains to the sacrificial meal, viewed as a social act, received particular emphasis from certain ancient customs and ideas connected with eating and drinking. According to antique ideas, those who eat and drink together are by this very act tied to one another by a bond of friendship and mutual obligation." (Robertson Smith 1889, 265)

> "The idea that kinship is not purely an affair of birth, but may be acquired, has quite fallen out of our circle of ideas… In Hebrew the phrase by which one claims kinship is "I am your bone and your flesh". Both in Hebrew and in Arabic, "flesh" is synonymous with "clan" or kindred group. To us this all seems mere metaphor from which no practical consequences can follow. But in early thought there is no sharp line between the metaphorical and the literal, between the way of expressing a thing and the way of conceiving it; phrases and symbols are treated as realities. Now, if kinship means participation in a common mass of flesh blood and bones, it is natural that it should be regarded as dependent, not merely on the fact that a man was born of his mother's

> body, and so was from his birth a part of her flesh, but also on the not less significant fact that he was nourished by her milk. And so we find that among the Arabs there is a tie of milk, as well as of blood, which unites the foster child to his foster-mother and to her kin. Again, after the child is weaned, his flesh and blood continue to be nourished and renewed by the food which he shares with his commensal, so that commensality can be thought of (1) as confirming or even (2) as constituting kinship in a very real sense." (Robertson Smith 1889, 273-274)

These discussions of the significance of nursing would be taken up again later (see Richards, below and section 8.6.3). It is also interesting to note the emphasis on local conceptions and the importance of symbols, which has since been re-emphasised as vital for the study of kinship by Schneider (1968, 1972, 1984) as well as by other cultural anthropologists (e.g. Geertz 1973). As Richards would later point out, Robertson Smith had an unusual definition of 'family' life (meaning presence of an adult male) which seems to undermine the significance of those statements just made about bonds between caregivers and children;

> "That the sacrificial meal was originally a kind of feast of kinsmen is apt to suggest to modern minds that its primitive type is to be sought in the family circle… But the notion that the clan is only a larger household is not consistent with the results of modern research. Kinship is an older thing than family life, and in the most primitive societies known to us the family or household group was not a subdivision of the clan, but contained members of more than one kindred. As a rule the savage man may not marry a clanswoman, and the children are of the mother's kin, and therefore have no communion of blood religion with their father. In such a family there is hardly any family life, and there can be no sacred household meal." (Robertson Smith 1889, 277-278)

This definition of family clearly ignores the question of social bonds between children and carers. The division between the kinship formed amongst male 'kinsmen' and that between children and carers is unhelpful if similar processes of bonding operate in the carer-child case as in the "between adults" case, as Malinowski, Richards and others suggest (see below). After Robertson Smith, further accounts of the significance of commensality are few until Richards (1932).

Crawley (1902) discussed commensality, but mainly to argue that in 'savage man' it does not exist since, as he would have it, man prefers to eat alone just like other animals (Crawley 1902, vol. 1). As well as being absolutely refuted by primatological evidence, this claim sits uncomfortably with his simultaneous suggestion, like Robertson Smith, that;

> "Food produces flesh and flesh is connected with blood… eating food together produces identity of substance, of flesh, and thereby introduces mutual responsibility resulting from eating what is part of the other, and giving the other what is part of oneself to eat." (Crawley 1902 Vol. 2, 121, quoted in Richards 1932)

Notice that sharing substance here emphasises the mutability of social identity, as opposed to the permanent 'shared genetic substance' concept prevalent in Euro-American kinship (Schneider 1968, 1984). This shared-substance (or consubstantiation) interpretation of eating together would also return in later discussions (see 8.7). Van Gennep (1960 [1908], 29) briefly mentions Robertson Smith's work when describing "rites of incorporation", but does not add anything of significance for kinship theory. Simmel's (1910) 'Sociology of the meal' also very briefly refers to Robertson Smith's finding on Semitic commensality (1997 [1910], 131), but mainly argues that sharing meals is a civilized 'triumph over the naturalism of eating' because it requires participants to observe 'temporal regularity' as well as individual restraint in taking a share of the food (Simmel 1997 [1910], 131).

Mauss's *The Gift* (1967 [1925]) also discusses the role of food sharing in maintaining social bonds, albeit mainly in the community wide and inter-community contexts. Richards (1932) would later classify this approach as 'Durkheimian' and argue for greater focus on the role of food sharing in creating social ties at the primary level (e.g. parent to child). Some of Mauss closely resembles Crawley's discussion of sharing substance;

> "To give something is to give a part of oneself… In this system of ideas one gives away what is in reality a part of one's nature and substance, while to receive something is to receive a part of someone's spiritual essence." (Mauss 1967 [1925], 10)

8.3 RICHARDS' HUNGER AND WORK

Richards' (1932) *Hunger and work in a Savage Tribe* reintroduced a focus on food sharing and in particular, a focus on infants, children and their carers;

> "Now the *nutritional system* of a primitive people is as complex and important as the *reproductive*, but the institutions centred round the biological need of food have never yet been described. It is this analysis that I want now to undertake. I want to examine the human relationships of a primitive society as determined by nutritional needs, showing how hunger shapes the sentiments which bind together the members of each social group. By what means is this fundamental biological want fulfilled in a given environment; and what forms of human activities and social groupings are so derived?" (Richards 1932, 23, emphasis in original)

> "We cannot analyse the formation of kinship sentiment in a primitive society unless we realize that the common sharing and preparation of food is one of the essential ties which hold together the groups, and one of the most important legal obligations of the family system." (Richards 1932, 28)

In contrast with Robertson Smith's subordination of 'family life' in favour of 'the clan', Richards, following Malinowski (1930b, see below), specifically focused on the family in her discussion of social bonding. Richards suggested that the same process of social bonding which contributes to the child's tie to its caregivers also underlies sentiments upon which later social bonds are built (see also Bowlby, chapter 7, and section 8.6.4);

> "…Family meals are intimately connected with the building up of ties of affection, confidence and trust towards the parents, and the sense of security and routine of home life." (Richards 1932, 28)

> "Primitive ritual shows clearly the extent to which the common meal becomes symbolic of the ties of union between two members of a group, and it is in the circle of the family household that these sentiments first begin to find shape." (Richards 1932, 60)

Richards (1932, 36-38) argues for the validity of a life-history approach in studying the formation of sentiments, and suggests a similar approach is visible in Malinowski (1930b), Radcliffe Brown (1922) as well as in Mead (1928). In reality, although the 'life history' approach may have characterised some of these accounts, Richards' interest in how social bonds are formed was all too unusual amongst anthropologists, with the exception of Malinowski (1930a; 1930b), whose interest turned increasingly towards 'biological needs' around this time (and who was Richards' tutor), but who didn't discuss potential mechanisms in any detail. Malinowski's view was that kinship ties are based on sentiments formed in childhood towards the parents, stemming from procreation, on the basis of the physiological care provided by them, and (like Richards) that clanship 'ties' are subsidiary;

> "As I have tried to show elsewhere, there is something almost absurd in the tendency of anthropologists to treat the family and the clan as equivalent units which can replace one another in the evolution of mankind. The relations between parents and child – that is, family relations – are based on procreation, on the early physiological cares given by the parents to the child and on innate emotional attitudes which unite offspring and parents. These elements are never found in clanship… It may be safely laid down that the family, based on marriage, is the only domestic institution of mankind, that is, the only institution the function of which is the procreation, the early cares and the elementary training of offspring. Kinship thus always rests on the family and begins within the family. The clan is essentially a non-reproductive, non-sexual and non-parental group, and it is never the primary source and basis of kinship." (Malinowski 1930a, 27-28)

As Schneider (1984, see chapter 9) later pointed out, Malinowski followed the conventional definition in his emphasis on the procreative basis for kinship sentiments, albeit also emphasising caregiving. In Richards' view, the best way to define a 'family' is precisely in terms of the regularity of eating meals together. Richards describes Zulu culture;

> "At mealtimes each different household is clearly distinguished, although the men and women usually eat apart. The members of family are those who receive their food from one woman, and who prepare it and eat it together according to the various rules of precedence which are observed in each particular tribe. Mr Bryant tells me that he has often heard Zulu mothers rebuke their children for straying into other huts at mealtimes,

> although by the laws of hospitality they would be bound to be offered food." (Richards 1932, 61-62)

> "[A child] becomes early acquainted with the grouping of the family at mealtimes, and the rules governing the ownership and distribution of cooked food. It is by lessons such as these that the whole kinship structure is felt rather than explained. Family sentiment is imprinted by a series of daily habits rather than taught by any definite lesson or rule." (Richards 1932, 66)

Here Richards expresses the view that it is the basic social environment, the one in which food is provisioned, which serves as the context of social and emotional bonding. However, like Malinowski (cf. Schneider 1984), she doesn't go so far as to question whether or not the procreative tie is necessarily 'the basis' for these acts of care and emotional bonds (see chapter 1). Richards also comments directly on Robertson Smith's claim about the primacy of clanship over familial sentiments (see above);

> "The clan grows out of the family and not the family out of the clan, and no society has yet been discovered of which it could be said that "there is hardly any family life at all". Field-observation has again forced a modification of earlier anthropological theories, and to my mind it is the sentiments formed in the intimate circle of the family hearth which are reflected in the sacrificial meal of primitive ritual. These sentiments can obviously only be understood through a first-hand observation of the daily life of the tribe." (Richards 1932, 180)

Nevertheless, following Robertson Smith, Richards also discusses the part played by nursing in mediating social ties – not just between the nurse and the infant, but also between those who have been nursed by the same person. Thus she notes Gutmann's finding that, for the Wachagga, "the bond of milk pledges you to stand by your brother" (Gutmann 1926, 254-7, quoted in Richards 1932). This connection is another emphasised by more recent ethnographies (see section 8.6.3). In sum, although not questioning the procreative assumption, Richards' approach is a unique synthesis of biological and sociological perspectives;

> "It was my thesis that nutrition in human society cannot be considered as a biological instinct alone, of the type that actuates the behaviour of the

> lower animals. Nor, on the contrary, can man's nutritive needs and food-getting activities be divided from the physiological basis on which they rest, as too often has happened in the history of sociological theory… [T]he earliest tie of childhood – that of the infant to its mother – is almost entirely a physiological relationship. The structure and bonds of the family in a primitive society are determined to a very large extent by the fundamental biological need of food: since it is within these groups that the child learns from whom he may expect his sustenance, and with whom it must be shared.
>
> But nutrition must also be considered from the sociological point of view. From the day of birth, tradition regulates the way in which the child is fed, and this process continues till adult life, the individual's choice of diet and manner of eating depending on the social customs and values of his tribe." (Richards 1932, 211-212)

8.4 WANING INTEREST IN FOOD SHARING

Richards' thesis, which greatly expanded on Malinowski's position in proposing food provision as mediating bonds, was subsequently referred to in positive language by both Firth (1934) and by Fortes (1936) in studies of the place of food in society. However, both (along with other anthropologists) nonetheless effectively ignored her focus on the significance of sharing food and the focus on the formation of social bonds and sentiments (see chapter 9 for further discussion of this neglect).

Despite Richards' persuasive account, the notion that social ties could usefully be studied in reference to social processes such as sharing food was thus largely ignored within comparative sociology and anthropology. An interesting exception is Cohen's (1955) *Cross-Cultural study of sharing and non-sharing*. This appears to be a rarely-cited work, probably due to its interdisciplinary nature, but it won an award at the time from the American Association for the Advancement of Science. Cohen's basic position is similar to Richards';

> "The reason for this apparently universal symbolic usage of food is that *food is the mainspring and the context of the very first warmth and sensed belonging – the very first sense of relation to another person – which the individual, as a neonate, experiences*. Generally speaking, the earliest experiences with the mother (as

> a representative of the world) through the instrumentality of food establish one important and basic pattern of relating to other people later on." (Cohen 1961 [1955], 330, emphasis in original)

Cohen also includes some interesting related points about how food sharing practices within a culture may affect what he calls the solidarity and communality of its social groups (see chapter 9).

For the most part, further study of processes of social bonding waited until the 1970s when, under the strain of mounting theoretical discussion questioning the utility of the genealogical 'kinship' approach to social bonding (see also chapter 1), some of these themes became more widely appreciated, and their practice investigated within societies.

8.5 SOCIAL BONDS THROUGH LIVING TOGETHER

Despite Richards' emphasis on social bonding at the level of individuals, most 'kinship' analyses continued to focus on the 'social structure' of groups. This group analysis combined with the emphasis on genealogical links is perhaps most clearly exemplified by the British 'Descent Theorists' (e.g. Radcliffe-Brown, Evans-Pritchard, Fortes) who placed a heavy emphasis on the 'descent reckoning' features of human societies and the primacy of genealogical lineality structures as *criteria for group membership* in the (typically African) societies they studied (see e.g. Kuper's 1982 review). Levi-Strauss approached kinship on a similar scale; his *The Elementary Structures of Kinship* (1969 [1949]) argued that an exogamy rule (an 'incest taboo') promoting exchange and alliance between potentially warring descent groups was the first act of culture. Levi-Strauss's argument was *explicitly* predicated on the notion that all other animals, including primates, have random mating and that "there is no regular pattern to be discerned in collective behaviour" (Levi-Strauss 1969 [1949], 6-7). We now know that almost all mammals practice exogamy, and that most primates have reliable social patterns (see chapter 5). On the genealogical question, Levi-Strauss did not explicitly discuss kinship as 'blood ties' apart from his reference to the culture of 'old ties of blood' in European 'houses' (cf. Carsten and Hugh-Jones 1995). He does however refer to 'the natural links of kinship'

(1969, 480 cf. Schneider 1984). Thus neither Levi-Strauss nor the decent theorists fundamentally questioned the primacy of genealogy.

The importance of *residence patterns* which passively shape the composition of social groups, notwithstanding supposed formal criteria such as ‘descent’ (and genealogy), has long been a submerged strand noted by students of kinship. In a recent review of this debate, Parkin notes that;

> “By the early twentieth century… it began to be realised that clans and other descent groups were frequently linked to a particular territory, however they were organised in other ways. Radcliffe-Brown, writing about Australian societies explicitly made the link between descent and territory, using the term ‘horde’ almost interchangeably with ‘clan’. This led some American anthropologists to challenge the idea of descent itself as a primary constituent of social groups. Alfred Kroeber, for instance, stressed residence and common economic activities (farming and so on). Robert Lowie (1920) and George Murdock (1949) turned the whole theory of descent around by claiming common residence as the basic factor, which gave rise to descent – that is, people did not live together because they were related by descent, but rather were related by descent because they lived together.” (Parkin 1997, 146)

These ideas about coresidence being a primary influence on subsequent kinship patterns in fact began to be aired not long after Morgan’s (1870) foundational work. Tylor (1889) observed that the lateral allegiances, succession and inheritance patterns so central to lineal descent systems would naturally follow from residence patterns, though he noted the lack of definitive data for his hypothesis. Lowie (1920) developed this position, highlighting also the influence of any sex-biased subsistence practice upon residence practice. Kroeber (1938) boldly suggested that “clan, moiety, exogamy, unilateral descent reckoning... are in a sense epiphenomena to other, underlying phenomena, such as place of residence.” (1938, 307) and that the former are not fundamental to human societies. Murdock (1949) also pointed to the primary influence of residence patterns, though largely maintaining the society-wide ‘structural’ analysis of kinship patterns. Aspects of his work has been continued by Ember and Ember (1971) and others who have further investigated the causal nexus around patterns of residence, subsistence, local warfare and lineality.

An important critique of the 'African models' of kinship and descent was Barnes' (1962) paper based on an analysis of social patterns and kinship in the New Guinea Highlands. This paper pointed out a number of exceptions to the descent models developed in Africa, including an emphasis on residence as opposed to 'descent' and also more focus on individual actions rather than society-wide structures.

Barnes pointed out that "the New Guinea hamlet is full of matrilateral kin, affines, refugees and casual visitors, quite unlike the hypothecated entirely virilocal and agnatic Nuer village (though similar to real Nuer villages)."(Barnes 1962, 5). (This critique of Evans-Pritchard's models was later repeated by Kuper; "Even the Nuer are not like *The Nuer*" (Kuper 1982, 84)). Barnes goes on to list a number of exceptions to a genealogical descent rule governing New Guinea social groups, including the point that "Many individuals who assert a mutual agnatic relationship are unable to trace out their connexions step by step and are uninterested in trying to do so."(Barnes 1962, 6). These observations led Barnes to suggest that;

> "[C]learly, genealogical connexion of some sort is one criterion for membership of many social groups. But it may not be the only criterion; birth, or residence, or a parent's former residence, or utilization of garden land, or participation in exchange and feasting activities or in house-building or raiding, may be other relevant criteria for group membership." (Barnes 1962, 6)

The predominant conception of 'kinship' as genealogical ties continued however, despite Barnes' findings. Fortes (1969) referred to "the irreducible genealogical connections, the given relations of actual connectedness, which are universally utilised in building up kinship relations and categories." (Fortes 1969, 52, see also A. Strathern 1973 and below). Nevertheless, the shift away from focus on genealogy towards the notion of 'kinship as co-residence' became stronger as other New Guinea ethnographies also emphasised that ties may arise from living together;

> "*The sheer fact of residence in a Bena Bena group can and does determine kinship.* People do not necessarily reside where they do because they are kinsmen: rather they become kinsmen because they reside there." (Langness 1964, 172, emphasis in original, quoted in Meigs 1989, 37)

8.6 CURRENT ETHNOGRAPHIES

8.6.1 THE EMERGENCE OF PROCESSUAL ACCOUNTS

As these non-genealogical conceptions of social bonding became more apparent, it was perhaps only a matter of time before more ethnographers began to reflect a combination of these ideas in their accounts. For example, Strathern (1973) noted the importance of both living together and sharing food as 'creating kinship' in New Guinea;

> "[F]ood, in fact, we may suggest, is a mediator between locality and kinship. A clear case is found in the Maring, among whom: 'First generation non-agnates in residence are usually considered members of other clans. Their children, however, appear to be considered members of the clan with which their father resides. The rationalisation for this is that these children have been nourished by and grown on the products of local land and therefore may be claimed as members of the clan' (Lowman-Vayda 1971: 322). I interpret this rationalisation as follows. Clansmen are felt to share identity. One way of symbolizing this is in terms of descent constructs (see Lowman-Vayda 1971). Such constructs posit that clansmen share substance in some way through their descent from an ancestor. Another way in which they share substance is through consumption of food grown on clan land. Food builds their bodies and gives them substance just as their father's semen and mother's blood and milk give them substance in the womb and as small children. Hence it is through food that the identification of the sons of immigrants with their host group is strengthened. Food creates substance, just as procreation does, and forms an excellent symbol both for the creation of identity out of residence and for the values of nurturance, growth, comfort and solidarity which are associated with parenthood." (Strathern 1973, 28-29)

The use of the concept of 'substance' here is somewhat similar to that of Holy (1996, see chapter 1.4). The utility of this usage has since been questioned (see 8.7). However, Strathern's emphasis on the symbols of shared food, shared residence and nurturance are very different from traditional kinship accounts. From the 1970s onwards, an increasing number of reports emerged which no longer assumed the primacy of genealogical ties in the construction of kinship bonds. Instead, these ethnographies attempted to give a cultural account of patterns of social bonding. Schneider's 1968 *American Kinship: A cultural account* provided an important impetus to this shift (see chapter 1). A key goal of this approach is to describe how the people themselves conceive of social bonds and their meaning. In the sections that follow, I review a number of such ethnographies.

8.6.2 CONNECTIONS BETWEEN CHILDHOOD AND ADULT BONDS

A typical feature of such accounts is the (previously neglected) emphasis on the process of formation of bonds from infancy and childhood onwards, rather than the traditional holistic emphasis on the 'kinship group'. As reviewed in chapter seven, Bowlby maintained the position that the mechanisms which mediate social bonding in adulthood are in many ways continuous with those that operate during infancy and childhood. Thus, treating adult social bonds as analytically distinct from childhood bonds may not be useful. Indeed, echoing this perspective, several ethnographers have reported that the processes mediating social bonding in infancy form the basis of those operating between adults ('kinsmen') in the wider social group. This is the case in Witherspoon's influential account of *Navajo Kinship and Marriage* (1975);

> "The Navajo never mention common substance in finding or invoking kinship ties or norms. Kinship is defined in terms of the acts of giving birth and sharing sustenance. The primary bond in the Navajo kinship system is the mother-child bond, and it is in this bond that the nature and meaning of kinship become clear. In Navajo culture, kinship means intense, diffuse, and enduring solidarity, and this solidarity is realized in actions and behaviour befitting the cultural definitions of kinship solidarity. Just as a mother is one who gives life to her children through birth and sustains their life by providing them with loving care, assistance, protection, and sustenance, kinsmen are those who sustain each other's life by helping one another, protecting one another, and by the giving or sharing of food and other items of subsistence. Where this kind of solidarity exists, kinship exists; where it does not, there is no kinship." (Witherspoon 1975, 21-22)

> "The ideal of communalism comes most directly out of the cultural definition of the mother-child relationship, which is realized in acts of

> giving and sharing. The mother-child bond is the primary bond of kinship in the Navajo cultural system and all kinsmen are essentially mothers and children to each other. If the Navajo have a golden rule, it would be, "One should treat everyone as a kinsman." This ideal is expressed in the fact that everyone, even a stranger, is addressed with a kinship term. The negative side of this is that one of the worst things one can say about another person is, "He acts as if he had no kinsmen."" (Witherspoon 1975, 95-96)

Witherspoon further re-emphasises this symbolism the final paragraph of his book;

> "The solidarity of mother and child, symbolized in patterns of giving life and sharing items which sustain life, is projected in Navajo culture as the ideal relationship between and among all people. All one's kinsmen are simply differentiated kinds of mothers; and, since everyone is treated and addressed as a kinsman, all people are bound together by the bond of k'e ["love", "kindness", "peacefulness", "friendliness", "cooperation"]… the k'e that exists between mother and child provides the foundational concepts and forms for all relationships in Navajo social life." (Witherspoon 1975, 125-126)

Further ethnographies give a similar account of the continuity of processes of bonding across childhood and adulthood (see below 8.6.4). Another reason why a focus on childhood bonding is probably not usefully separated from conceptions of adult social bonds (e.g. between 'kinsmen') is that, in many circumstances, an adult's most significant social bonds may be those first formed during childhood and infancy (see also chapter 7.4.5). Gow's (1991) account of 'kinship' in the Peruvian Amazonian Piro demonstrates that the strongest social bonds for adults are frequently said to be those which were formed during childhood. This includes bonds to the individual's caregivers, and bonds between those that were 'raised' together;

> "[A] person may be real kin to Ego's real kin, but not necessarily real kin to Ego. This is not because native people think in terms of group boundaries or of genealogical relations, but rather because they think in chains of relationship of raising and being raised together… When people talk about their real kin, they make continuous reference to the past, and particularly to their childhood. This is clear from the idiom of caring

> discussed in the previous section, but it is pervasive in discussions of real kin. One man described his attachment to his uncle as follows, 'When I was a child we lived together down on the Ucayali. He was always good to me, and brought us food. He loved me a lot.' The most intense of such relations of memory are those between parents and children. Adults constantly evoke their own childhood, and the care they received from their parents, as a reason for wanting to be near them." (Gow 1991, 164,167)

As Witherspoon points out for the Navajo (see above) so for the Piro too, peers can be caregivers to one another; thus a distinction between those who give care and those who one is raised with may not always be appropriate. Early caregivers may simultaneously be older siblings;

> "As a child begins to eat real food, and to walk and eventually to talk, its relationship to its parents changes from one in which the parents take care that their physical connection to the body of the child does not harm it, into one in which gifts of food, given out of love for the child, evoke the child's love for its parents and other kin. Older siblings are very important here. From birth, the baby is frequently picked up and held (*marcar*, 'to hold in the arms') by its older brothers and sisters. As it learns to walk and talk, its closest physical ties are with such siblings, for they are its constant companions and they eat and sleep together. Such intimate ties with siblings replace the earlier one with parents as the child grows." (Gow 1991, 157)

Here, Gow's account also suggests that spending time together ('constant companions'), sleeping together, as well as sharing food and eating together are the experiences that constitute being 'raised together'. These kinds of interaction (which were discussed in chapter 7) figure for other societies, as we will see below.

8.6.3 A FOCUS ON CHILDREN AND CAREGIVING

Recent ethnographies often report social bonds between individuals in terms of sentiments, love and attachment. At the same time, it is the processes that create such bonds which are emphasised, including aspects that were perhaps underemphasized by Bowlby (see chapter 7). Perhaps the greatest difference between these ethnographic accounts and earlier discussions of kinship is the focus on the lives of children, and a 'micro' account describing daily living arrangements and various repeated processes of interaction. De Matos Viegas (2003) notes that for a Caboclo-Indian community of south Bahia, Brazil;

> "[T]he attachment between parents and children becomes meaningful not only because events of significant content are taking place, but also because the same actions are continually repeated every day… I argue that by focussing on the intersubjective relations whereby kinship is constituted, time as a dimension of sociality becomes apparent. Time is explored in this article from two ethnographic perspectives. I show, first that, in order to become kin, people need to keep on repeating small acts such as dressing or feeding, both daily and on a continuous basis over days, weeks, and months, and, secondly, that people can turn others into kin by performing such acts. But the latter makes even clearer the importance of this daily re-enactment with relation to the forming of kin links. It shows that people are deeply aware of the fact that, if they stop performing these acts, the link between parents and children is weakened, and may even be severed altogether." (de Matos Viegas 2003, 22)

As Gow suggested for the Piro (see above), de Matos Viegas finds that adults remember those who spent time in raising them;

> "Adults who early in their lives had been taken to become raised children [fostered] state clearly that the situation had never displeased them. They maintain that they belong to the woman who cared for or raised them, and it is to her that they want their children to become attached. Although they recognise who their *pais legítimos* are, it is those who have cared for a person for a longer period of their childhood that are considered mother and father. It is in this sense that kinship is constituted as memory of being related through caring and feeding, along the lines developed in large part by Peter Gow and within other South Amerindian contexts." (de Matos Viegas 2003, 32)

Other reports from South America give a similar view. Weismantel's influential (1988) study of Zumbagua society demonstrates a 'house and hearth' theme which would be taken up by Carsten and others later (see below). She finds that;

> "In Zumbagua, the hearth defines the home. It supplants the marriage bed as the symbol of conjugal living and the bond of blood as the emblem of parenthood: the Zumbagua family consists of those who eat together. The hearth's importance can be seen in the great significance attached to the founding of a new kitchen. A man and woman are ready to marry after a year's courtship, but it may be ten years before they begin to cook apart from their parents and siblings." (Weismantel 1988, 169)

> "On a day-to-day basis, then, the use of parent-child terminologies refers to the people who share a hearth: the older generation that feeds and the younger one that is fed. All of the children that a couple raise in their household (*vinachishka*) are referred to by them as their sons and daughters. Food, not blood, is the tie that binds." (Weismantel 1988, 171)

Like de Matos Viegas, Weismantel also emphasises that the process of creating social bonds involves time and daily contact, and also reflects living arrangements;

> "The emphasis on work and time that undergirds the Zumbagua kinship system exposes the material bases of social reproduction. Parenting is a long and often collective process by which a helpless and prelinguistic infant – not even human in the Andean definition of the concept – is shepherded past the illnesses that kill thousands of indigenous children each year to become, first, a Quichua-speaking subject and, later, a parent. In this context the physical bond between parent and child is not characterized in the essentialist (and oddly non-physical) terms of an involuntary genetic connection that exists even if undiscovered, but, rather, this bond is forged through far more sensuous connections created through taste, smell, and touch. The purchase of foods with scarce funds, the gift of warm clothing in a cold climate, the intimate familiarity with each another's body that comes from sleeping, bathing, and eating together in the close quarters of a one-room house: these are the material bases of kinship in Zumbagua." (Weismantel 1995, 707-708)

Where Weismantel echoes Richards in emphasising shared eating within the household, the theme is continued by Carsten's work in Malaysia. Carsten's work also gives us an interesting insight into the use of the concepts of *substance* and *consubstantiation* in descriptions of social bonding and 'kinship'. As will become clear in the quotes and the commentary, despite superficial similarities, this 'substance' has a very different meaning from the 'biogenetic substance' of Euro-American kinship (Schneider 1968, 1984), in short because it is 'mutable' (see chapter 1.4, and 8.7 below). Whilst Carsten continues the notion of the shared hearth as the focal point of the house and its members, she particularly emphasises the importance of sharing rice meals prepared on the hearth, and the 'shared substance' and even 'shared blood' that this creates;

> "In this article I analyse the cultural construction of kinship among Malays on the island of Langkawi. Amongst these Malays ideas surrounding co-eating and sharing are as fundamental for kinship as are ideas about procreation… Eating together implies having blood in common. One becomes related to the people with whom one shares consumption. And these may or may not be one's genetic kin. In other words, although one is born with blood, one's blood also becomes. The substance of kinship is acquired in the course of childhood through developing social relations in the house." (Carsten 1991, 425-426)

> "In particular, houses never have more than one hearth, *dapur*. However many couples reside together in one house, they always cook and eat full meals, of which rice is a main constituent, together. This commensality is a prime focus of what it means to be of one household." (Carsten 1991, 426-427)

> "Through the day-to-day sharing of meals cooked in the same hearth, those who live together in one house come to have substance in common. From this point of view, eating such meals in other houses has negative implications, and children are strongly discouraged from doing so. Eating meals in other houses implies a dispersal of intimate substances to other houses… In a culture in which people often move to other houses, these ideas gain further salience. The frequency of divorce, and temporary or more permanent fostering, lend an enormous force to the idea that living and eating together is one way of coming to share substance. This has further significance, however, in the historical context of demographic mobility characteristic of Langkawi. Feeding is one way in which strangers and outsiders can begin their incorporation into a village community, a process that continues with fostering and marriage. The converse process means that if close kin move to the mainland or to other villages in Langkawi and cease to interact (either because of geographic distance or quarrels) their kinship and that of their descendants effectively lapses." (Carsten 1995, 234)

Like Gow and Weismantel, Carsten also notes the emphasis placed on the child's sleeping in a particular house (Carsten 1991, 429). The concept of consubstantiation here, even as 'shared blood', is one that is mutable; open to continuous transformation and 'environmental influences' (thus the importance of eating in one's own house rather than in others). It is not just rice-meals which contribute to substance, nursing-milk also does;

> "Feeding is said to begin in the womb. In its first house the child is nourished by its mother's blood. After birth, the milk fed to a baby from its mother's breast is believed to derive from the mother's blood. People say that "blood becomes milk," *darah jadi susu.* The mother's milk is immensely important to a child's physical and emotional development and to the child's connection with its mother. Children who are not breast-fed supposedly become ill; they may also fail to "recognize" their mothers." (Carsten 1995, 227)

> "The substance that kin are said to share derives in large part from the shared consumption of milk as babies… In the context of widespread fostering arrangements of different kinds, co-feeding can create shared blood, shared substance, and kinship. People in Langkawi say, "If you drink the same milk you become kin," *kalau makan sama susu, jadi adik-beradik.* "You become one blood, one flesh" *jadi satu darah, satu daging*… There exists a continuum between rice (food), milk, and blood. The sharing of any or all of these connotes having substance in common, hence being related." (Carsten 1995, 228)

The importance attached to the consumption of these various 'consubstantiating' foods, and to where one sleeps, clearly demonstrates that a child's social identity is mutable and open to influence rather than given (see also Carsten 2001). Montague (2001) also describes how sharing mother's milk constitutes 'relatedness' in the Trobriand Islands;

> "Early on in my doctoral fieldwork I caused a group of women to roll on the ground laughing when I suggested that Westerners think that people are related because they share blood. (I did not know any way to couch the words "biogenetic substance" in the Trobriand language, so I had to fall back on tradition.) Finally, one of the women recovered herself enough to gasp out, "No! People are related through mother's milk!"…

> [T]he newborn may not be nursed by its genetrix, but by some other woman instead. " (Montague 2001, 174-175)

Montague, like Carsten, uses the concept of sharing mutable substances that parallels conceptions of changeable social identity. As we have seen repeatedly, the emphasis here is on performance and process as is made clear by the similar importance of later food provisioning by the ina/'mother';

> "Thus we confront the fact that, for example, even if ego's *ina* (Malinowski's "mother") *is* ego's genetrix, she is not ego's *ina* by virtue of *being* ego's genetrix. She is ego's *ina* by virtue of *deciding* to provide the child with processed staple and nonstaple foods. If ego's genetrix never provides ego with processed foods, she never becomes ego's *ina.* Moreover, if, having provided ego with processed foods, she decides to stop doing that at any time during ego's minority, she ceases to be ego's *ina.* As Bosiwosi put the matter, "Gala ina. Besa bogwu aokuva" (Not *ina.* This is already over)." (Montague 2001, 176)

Other ethnographies, whilst emphasising the same processes as mediating social bonds, suggest that we should focus on the 'performance' of the nurturing behaviour, rather than the more material 'state of connectedness' that substance implies. Thomas' (1999) work on the Temanambondro of south east Madagascar discusses potential drawbacks of the emphasis on substance (see below 8.7) and instead points to the ongoing giving and receiving of nurture;

> "[W]hilst procreation and birth do create some type of relation, this is not thought of in terms of substance. Moreover, the relation is hardly elaborated upon and in fact does not constitute kinship in any significant sense; it 'counts for' very little (cf. Schneider 1980:120-4). The reason for this, I suggest, is that procreation and birth are not the template for Temanambondro kinship. Indeed Temanambondro place emphasis on relationship constituted through practice rather than through procreation and bodily substances, as we will see presently." (Thomas 1999, 29)

> "Among Temanambondro it is not unusual for a man to marry a woman who already has a child. Upon completing the marriage rites, the man may negotiate with his 'in-laws' (*rafoza*) to have the child 'recognized' as his own regardless of whether or not he is known to be the father who 'gave

> birth to' the child. Indeed it is sometimes well known that he is not, but if the child is subsequently 'recognized' as his own then he becomes the child's father and the child takes on his ancestry identity." (Thomas 1999, 35)

> "Yet just as fathers are not simply made by birth, neither are mothers, and although mothers are not made by 'custom' they, like fathers, can make themselves through another type of performatively constituted relation, the giving of 'nurture'. Relations of ancestry are particularly important in contexts of ritual, inheritance and the defining of marriageability and incest; they are in effect the 'structuring structures' (Bourdieu 1977) of social reproduction and intergenerational continuity. Father, mother and children are, however, also performatively related through the giving and receiving of 'nurture' (*fitezana*). Like ancestry, relations of 'nurture' do not always coincide with relations by birth; but unlike ancestry, 'nurture' is a largely ungendered relation, constituted in contexts of everyday practical existence, in the intimate, familial and familiar world of the household, and in ongoing relations of work and consumption, of feeding and farming. " (Thomas 1999, 37)

Thomas suggests that performance is what actually creates the relationship for the Temanambondro, and parentage by birth is not the issue, even in the mother-child case. Schrauwers' (1999) study of the Pamona of Central Sulawesi, Indonesia provides a similar view. Schrauwers emphasises process and suggests that, even in the case of the affective ties between parent and child, it is 'time and effort' that make the relationship, not any genetic connection;

> "The ease with which children move from house to house reflects a notion of parentage rooted in nurturance and shared consumption, rather than narrowly defined biological filiation. The personal acknowledgement of parentage is more closely linked to affective ties established through actual coresidence and shared consumption (cf. Carsten 1991, Weismantel 1995)… Whereas to Pamona, parents and children see the recognition of parentage as emergent through time and effort, Westerners' kinship theory of parenthood is inherently structural and timeless, determined by the single moment of conception (Weismantel 1995:697). Kinship theory requires a processual approach to parentage that recognizes it as a "transaction in kinship" (Brady 1976). Parenthood, no less than adoption

> and fosterage, is negotiated situationally, not established by nature." (Schrauwers 1999, 311)

These reports strongly suggest that various regularly occurring contexts, and particularly the performance of nurturing behaviour are crucial to social ties in the parent-child (and child-child) cases. But what about the creation and maintenance of social bonds between adults?

8.6.4 PERFORMING NURTURE: CARING AND SHARING BETWEEN ADULTS

Witherspoon reported that, for the Navajo (see above 8.6.2), the performance of care and nurture not only underlies social bonds between adults and children, but also between adults and adults. Stafford, working in Dragon-head village, North Eastern China, and Angang, Taiwan, demonstrates that the care given by adults to children creates social bonds and an enduring respect which is then typically returned to the carers as elderly dependents when the children becomes adults themselves;

> "*Yang* is a very common Chinese expression meaning 'to raise' or 'to care for', e.g. in 'raise flowers' (*yang hua*), 'raise pigs' (*yang zhu*), or 'raise children' (*yang haizi*). In the case of children, the provision of *yang* – a kind of all-encompassing nurturance – is, of course, very complex. It is also productive of an almost inescapable obligation: once they have grown up, children are heavily obliged to *yang*, 'care for', or *fengyang*, 'respectfully care for', their parents in old age. More specifically, the receipt of *yang* from one's parents during childhood obliges *sons* to return *yang* to their parents later in life… [however] it is women who normally shoulder (often 'on behalf of' their husbands) the actual process of providing *yang*; in many cases for their parents-in-law, their parents, their children, and their grandchildren." (Stafford 2000, 41-42, emphasis in original)

Stafford suggests that defining the content of *yang* is not straightforward, but includes the provision of housing, clothing, education, and money, as well as food. Stafford goes on to note that *yang* can create relatedness independently of genealogical ties;

> "It is possible to produce, through *yang*, relatedness with children who are not one's own 'natural' descendents. Children raised by foster parents (called *yang* mothers and *yang* fathers) are obliged, *because* they have received *yang* from them, to care for their foster parents in old age… [correspondingly] there are many cases in which a failure of the 'cycle of *yang*' is what provokes the termination of relations of descent. Sons who fail to provide their parents with *yang* may be dropped from family estates, ties of blood notwithstanding. In sum, *yang* may produce kinship where there is no 'natural' tie of descent, and the absence of *yang* may end kinship where a 'natural' tie exists." (Stafford 2000, 42-43)

Stafford's description of the cycle of yang is reminiscent of Schneider's description of changing care and dependency in the *citamangen* / *fak* relationship on Yap (Schneider 1984, see chapter 1.2). Stafford suggests that this perspective may be important for Chinese ethnography since the heavy emphasis on descent has, he suggests, perhaps obscured fundamental similarities in the basic workings of 'kinship' between Chinese society and others;

> "[T]his cycle – through emphasis on feeding, nurturance, and care – is comparable (as I have mentioned) to the processual, fluid, and transformative forms of kinship which anthropologists do *not* generally associate with China… Not surprisingly, the reality is that in China, as elsewhere, people *make* kinship – it is, of course, never simply 'given' to them by birth – and patrilineal ideologies, however powerful, are forced to compete in a crowded field of ideas about the ways in which relatedness is produced." (Stafford 2000, 43, 52)

There is common sentiment amongst southern Chinese, *遠親不如近鄰* - 'distant relatives are no better than close neighbours' reflecting the point that patrilineal ideologies are not always necessarily as prominent as many accounts would suggest, and that coresidence may be more important (see also Vilaca 2002, Storrie 2003, below).

Marshall's influential studies of the Truk District, Caroline Islands, Micronesia (now known as Chuuk) also suggest that ties which are created and maintained through caring and nurture are not limited to those between adults and children, but also between adults;

> "Trukese kinsmen are those who share such things as land, labor, residence, support, and (not necessarily) genetic substance who choose mutually to acknowledge each other as kin. In the Trukese view, those who nurture one another through acts of sharing *validate* their natural kinship or *become* created kinsmen as a consequence of these nurturant acts. It follows from this that persons who do not continue to nurture each other may cease to recognise each other as kin (compare Carroll 1968:7, 1970b:147; Smith 1977:477-478). For Trukese, then, kinship is "active" - it must be sustained by continuing nurturant behaviours." (Marshall 1977, 650-651)

> "Like any other social system, Trukese society contains a limited set of relationships to which individuals feel a very strong sense of commitment, which are characterised by a high degree of affect and sharing and which endure over time. In GTS [Greater Trukese Society], these intensive interpersonal relationships generally include some or all of the following features: intense commitment, complete trust, diffuse reciprocal obligations coupled with explicit rights and duties, intimacy, confidentiality, privateness, and regular unquestioning mutual aid, support, and cooperation. Features such as these receive expression in different cultures in a variety of distinct ways, but they all reduce to one central idea: sharing. This includes the sharing of time, things, thoughts, and these, in turn, are represented symbolically by a broad range of possibilities. Shared substance, shared residence, shared food, shared land, shared locale, common names, and a variety of other alternatives have been selected by different cultures to symbolize the essence of "intensive interpersonal relationships". No matter what symbols are chosen, however, one thing remains constant: close personal relationships involve the concept of sharing." (Marshall 1977, 654-655)

> "All sibling relationships – natural or created – involve the height of sharing and *ttong* "feelings of strong sentimental attachment."… In Trukese kinship, actions speak louder than words; *ttong* must be demonstrated by nurturant acts. Trukese kinship pivots on the fulcrum of nurturance, a fact partially understood by Ruth Goodenough (1970:331) who noted the "intense concentration on problems of nurture – taking care of and being cared for by others" in GTS. Nurture is the nature of Trukese kinship." (Marshall 1977, 656)

More recent ethnography confirms this view of the process of social bonding in Truk (now Chuuk). In a paper explicitly focusing on the continuity between attachment theory and the social bonds of 'kinship', Lowe (2002) reiterates that;

> "The point here is not that "real" kin relationships are genealogical whereas "created" kin relationships are based on interpersonal histories of reciprocal acts of assistance and nurturance. *All social relationships in Chuuk are defined, in part, by the quality of mutual acts of nurturance and support.*" (Lowe 2002, 128, emphasis in original)

Vilaca (2002) suggests that, for the Wari people of Western Amazonia, Brazil, these same processes of the performance of mutual care, sharing food, and the daily context of living together are what underlie social and emotional bonds for adults as well as children, just as they do in other Amazonian groups;

> "The performative aspects of kinship are present in numerous Amazonian ethnographies. Notions such as the cognatization of the local group, found in studies of Guianese groups (Overing 1975; Riviere 1984), and others (Gow 1991: 192), point us to a similar inference; people who live together tend to be identified as consanguinal kin, whether through the use of consanguinal terms of reference or through the use of teknonyms." (Vilaca 2002, 351)

> "Kinsfolk, Called *ka nari wa*, may be classified as true kin, *iri nari*, and distant kin, *nari pira* or *nari paxi* (where *iri* means true, *pira* means 'far' and *paxi* means 'more or less'). Though on some occasions the Wari' say they are all kin, they tend to classify cohabitants as true kin and those who live at a spatial or social distance as distant kin. The closest *win ma* are same sex siblings, but the term is usually extended to include all inhabitants of the local group and members of the sub-group, such that the term *win ma*, which means 'one who accompanies' or 'one who does the same', functions as an antonym of foreigner, *tatirim*. Today, the Wari' usually refer to inhabitants of the same post (a village settlement, equivalent in actuality to a sub-group) as their true kin and on these occasions may exclude genealogical kin who live in another village." (Vilaca 2002, 352)

Vilaca points out that this emphasis on coresidence occurs in other Amazonian contexts, and cites Gow's work with the Piro (see above). She also points out the contrast between this conception of 'kinship' and what she calls 'our own ideas';

> "The same type of phenomena was described by Gow in terms of the Piro: proximity and living together are so decisive in determining kinship that genealogical kin who live far away may be excluded from the kin circle. Inhabitants of the village of Santa Clara would very often say: 'we are all kin here'. And a woman once told the author: 'These are my kin, the people in this village. You know them all, there are no others.' According to Gow, her statement excluded two siblings, two daughters and many other real kin in other communities, while simultaneously including several people with whom she otherwise counts no close kin connections at all' (1991, 193-194). It should be stressed that this is not a purely formal or terminological assimilation, but a true process of consubstantialization, generated by proximity, intimate living, commensality, mutual care, and the desire to become kin. For many Amerindian groups, the body is a product of particular social acts that continually transform it. This implies a radical difference in focus: in contrast to our own ideas, informed (at least from the end of the nineteenth century) by a genetic conception of kinship in which substance determines social relations, in Amazonia, social relations determine substance (Viveiros de Castro 2000: 29 n.40, 30)." (Vilaca 2002, 352)

Here again we see the substance theme, but as Vilaca suggests, and is made clear by Storrie (below) the difference is that this concept of substance is of something transformable, not immutable down the generations. Storrie's work (2003) on the Hoti of Serrania de Maigualida, Venezuelan Guiana, again finds that living together, being raised and nurtured together, and sharing foods creates strong bonds of affection and sentiment (see also quotes in next section 8.7);

> "The existential framework and sense of well-being that Hoti derive from everyday relationships stand in place of what we call 'kinship', and this is a matter of the interaction of distance and sentiment… As I have already indicated, there is no interest or concern among the Hoti about any possible genealogical basis for their relationship terminology. The important thing is whom one lives with. How one came to live with these people is largely unimportant" (Storrie 2003, 416)

> "It was my Hoti friends who, through their rejection of my expectations that I would be able to 'collect' genealogical information, brought me to the idea that dwelling together and particularly the notions of

> consumption and ingestion are, for them, fundamental to social identity. Whenever I attempted to discover if there were ideas of genealogical relatedness between kin, I was told that there is nothing that links a parent to their children, or siblings to each other, apart from the bonds of affection and sentiment that they feel for each other. In other words, there is nothing more to 'relatedness' than those things that link 'all people' together." (Storrie 2003, 420)

8.7 CLARIFYING 'SUBSTANCE': TRANSFORMABLE NOT FIXED

Storrie's account of the sharing of substance in Hoti culture clearly demonstrates the distinction between this form of substance and the 'biogenetic substance' conceived of as central to Euro-American notions of kinship (see also chapter 1.4, and 8.6.3 above);

> "Kin are bound together by ties of shared physical and metaphysical substance, but this is not transmitted by descent. The transferable property of substance is further reflected in the morality of sharing. The most obvious thing that kin do amongst themselves is to share, and the most obvious thing they share is food. Sharing food, over time, transforms the unrelated into the related. This sense of shared substance is very strong among those who have been raised and nurtured together, but the transformative effect of sharing food and living together is made clear also in the case of pets, who can become kin.
>
> The idea that food, and particularly meat, is imbued with a certain agency is quite explicit for the Hoti. I was told that 'when you eat tapir meat, you become a little bit tapir'. The weakest, most vulnerable and most transformable 'eater' of meat is the unborn child. For this reason, the majority of dietary restrictions apply to pregnant women. However, restrictions also apply, to varying degrees and depending entirely upon personal sentiment, to members of the pregnant woman's kin, as all members of this group are linked together through their shared substance, and thus are capable of affecting and transforming each other. For the Hoti, people are grown through the participation of others and the mixing of substances – not just in the womb but for all of their lives. Here, crucially, the substances that are shared and mixed by kin are not pre-

> specified (as they would be in a genealogical model of relatedness) but are continually incorporated (literally embodied) through all of a child's kin. When food is offered to a guest or stranger, it is believed that the giver seeks to make the recipient like the giver. In accepting, the guest minimizes the difference between them. It is through this process that affines, and even strangers, may become kin. It is also why co-residence is so important, and why even close consanguines who are no longer co-resident are eventually forgotten, as their substance changes from shared to different." (Storrie 2003, 421-422)

Montague confirms this mutability of connecting substance also occurs in cases where individuals are conceived as sharing blood, as for the Trobriand Islanders;

> "The first food that any newborn child routinely ingests is mother's milk. Because mother's milk contains traces of everything that mother has ever consumed, and because, through digestion, mother's milk enters into the newborn's blood, the newborn child's blood becomes compositionally identical to that of the woman whose breast milk it consumes [not necessarily the genetrix]. The result is that this woman becomes its *veyotatu*, a person who has avoided consuming the same seasonal wind-related bird and plant foods of the air as has ego… [T]he substantial identity between any two *veyotatu*, is mutable. Either one of them can at any time consume some foodstuff which alters his bodily substance such that it is no longer sufficiently the same as that of the other for them to still be one another's *veyotatu*." (Montague 2001, 174-175)

In sum, all the current ethnographies which describe a concept of substance emphasise its transformable, non-fixed, 'open-to-environmental-influence' character. This 'substance' is thus the opposite of 'biogenetic substance', which is definitively fixed, given ('being'), and impenetrable to environmental influence. This distinction is also a major component of Ingold's (2000) discussion of 'substance' and the problems of prioritising genealogy over relationships of nurture. Partly because of its 'biogenetic' connotations, the utility of substance as an analytical concept has recently been questioned by some theorists (Thomas 1999, Carsten 2001). For example, Thomas (1999), notes the frequency of use of the concept, and comments that;

> "Whilst I would accept that the term is not without its merits, and that some very sophisticated analyses of kinship in terms of substance have been made, I think that there are also some problems with the use of the term. Aside from the fact that it risks perpetuating some of our own cultural preoccupations about the nature of kinship, as something rooted in bodies and conceptualised in terms of (ethno)biological processes, the term is sometimes used in such a way that it obscures rather than clarifies 'culturally posited forms of relatedness' (Schneider 1984: 117). Occasionally references to substance do not contain sufficient ethnographic detail for the reader to clearly ascertain what the term signifies in a particular instance, and all too often the explanatory power of the term is assumed rather than demonstrated." (Thomas 1999, 22)

As we saw above (section 8.6.3), Thomas prefers an explicit statement on what kinds of circumstances, behaviours and performance are involved in creating 'relatedness'.

8.8 SUMMARY OF THE FINDINGS

There are many other ethnographies which have not been quoted from that are resonant with the above reports, and can be consulted by anyone interested. Such ethnographies also document the importance of processes such as 'nurturing,' 'caring for' or 'compassion' (e.g. Meigs 1989, 1997; Toren 1999; Lambert 2000; Bodenhorn 2000; Zimmer-Tamakoshi 2001); sharing food (e.g. Watson 1983; Janowski 1995; Meigs 1997; Rival 1998; Toren 1999; Lambert 2000); sharing living environment (e.g. Watson 1983; Rival 1998; Lambert 2000); sleeping together (e.g. Pader 1993; Sault 1995; Rival 1998) and working together (e.g. Bodenhorn 2000; Nuttall 2000).

The recurrence of these themes in so many ethnographies, from such a wide range of cultures has led to suggestions that, despite exorcism of genealogical assumptions, some cross-cultural commonalities could nevertheless be said to underlie the formation of 'kinship' bonds. Galvin (2001) makes such a suggestion;

> "Recent research differs from much earlier work in that it refuses to take for granted the underlying assumption of the biological basis of kinship, but at the same time, this new research does not follow the call to

> abandon or dismantle kinship in anthropology… based on this recent research, this chapter suggests that not only is kinship a valid field of study, but also that some bases for the cultural construction of kinship may be universal." (Galvin 2001, 109)

Galvin draws upon the ethnographies of Carsten and Weismantel (see above) as well as Parish (1994), and points to food sharing and living together (sharing of shelter) as potentially universal components;

> "[T]hese contemporary kinship researchers have also found ways to explore and describe kinship systems. They accomplish this by illustrating other ways that people create "kinship" amongst themselves. Yet they all appear to have in common the idea that substance of sharing, of life-giving or life-sustaining properties, is necessary in one form or another to forge bonds of kinship. All three use food as a medium through which relatedness is constructed… [T]he other type of sharing is the sharing of shelter. Like food, shelter is sometimes no more complex than its physical characteristics, and at other times, is represented by more intangible properties of space. Although in the Langkawi group, rice, as food, is both conduit and sustenance, it also takes on kin constructing qualities from the hearth. Rice eaten where food is shared is as vested with the ability to create relatedness as other substance." (Galvin 2001, 118-120)

Here then is an account that also notes some of the potential common threads in reports of the cultural conceptions of kinship. Even cognitive approaches to kinship terminology (which are perhaps closest to evolutionary psychology approaches) have drawn similar conclusions;

> "In constructing kin term meaning, children also rely on observed patterns of behaviour – specifically, the enduring and habitual associations having to do with the sharing of sleeping, eating, and other sustenance relations typically grouped under the rubric of coresidence. This appears to be true of adults as well as children, though most cognitive accounts of kinship have ignored this aspect of the kinship concept." (Hirschfeld 1994, 221)

In sum, the above ethnographic reports seem to reliably demonstrate that social and emotional bonds are very often mediated by processes and circumstances rather than by genealogical relatedness *per se*, over a wide range of human cultures. Many of these peoples place little or no cultural value on genealogical links, and others, whilst placing variable cultural value on genealogical links (not necessarily underscored by a Euro-American concept of procreation), may nevertheless consider such links revocable rather than inalienable, where acts of nurture and care are absent (see, e.g. Stafford 2000, above).

Further, there is a definite compatibility between the processes conceived of as mediating social bonds, as described in these ethnographic reports and social bonding mechanisms described by attachment theorists (see chapter 7). In some cases this compatibility between ethnographic treatments and attachment theory is made explicit by ethnographers. This theme will be looked at further in the next chapter.

CHAPTER NINE – SUMMARY AND DISCUSSION

9.1 INTRODUCTION

The previous chapter reviewed ethnographic reports and found substantial support for the notion that various nurturing processes and circumstances create social bonds notwithstanding genealogical links. This demonstrates that cultural approaches to understanding the formation and operation of social bonds (or 'kinship') in a variety of societies are compatible with attachment theory's findings on the formation of social and emotional bonds and, by extension, compatible with the basic biological theory of social behaviour.

A focus on personal attachments and emotions has been a submerged strand in kinship theorising at least since Malinowski and Richards (see previous chapter). Other than the current research, other recent analyses have discussed the compatibility between attachment theory and ethnographic findings on kinship; to compliment the review in chapter eight, we start by discussing this trend in section 9.2. I argue further, that ethnographic accounts are extending our understanding of attachment and social bonding processes beyond the perspectives of traditional attachment theory and research.

I then conduct a brief review and summary of the steps of the argument made in chapters one to eight, emphasising the distinctions between the current interpretation of basic theories, and more traditional interpretations (see sections 9.4 & 9.5).

Section 9.6 draws upon some of the insights afforded by the current analysis to consider some possible correlations of the 'blood is thicker than water' conception of the basis of social bonds, particularly prevalent in Euro-American culture. I suggest how other aspects of the cultural background (neolocality and economic individualism) may also contribute to the prominence of this symbolism.

In section 9.7 I suggest that ethnographic accounts of kinship can benefit from focusing on the local factors that shape patterns of social relationships. In a time of transformation of economies and community structure, what impacts can external influences have on the strength, flexibility and constancy of social ties? I briefly review examples of recent work which, I believe, strongly demonstrate the power of ethnographic analysis to document how historical, ecological, and political-economic influences shape patterns of social bonding, and how changes in these factors are implicated in social change. Examples of forces of globalisation and cultural diffusion from Western societies will be discussed here.

9.2 ETHNOGRAPHERS' STUDY OF INDIVIDUAL BONDS

In reviewing recent ethnographic material (chapter 8) we found that some analyses make explicit reference to individual social and emotional bonding processes, and occasionally even to psychological concepts such as attachment. In this section we review some recent related perspectives.

As was noted in chapter eight, Malinowski and Richards paid considerable attention to the development of social bonds in infants and children, and argued that such primary bonds are the basis of links across the wider group. These accounts were nevertheless accompanied by an emphasis on blood ties (see below). As pointed out by Carsten (2000), whilst others (e.g. Fortes) recognised that strong bonds are formed between children and caregivers, the connection with wider social ties (proper 'kinship') was played down by an analytical separation, and the latter social sphere was generally deemed to be of more interest;

> "The formalisation of kinship as a field of study involved the separation of what Fortes termed the 'domestic domain' from the 'political-jural domain' (1958, 1969). Both Malinowski and Fortes saw the nuclear family as a universal social institution which was necessary to fulfil the functions of producing and rearing children (see Malinowski 1930; Fortes 1949). They both had a keen interest in domestic family arrangements, which may in part be attributed to the influence of Freudian psychology (see Fortes 1974, 1977). Fortes also saw kinship as 'an irreducible principle', the source of basic moral values (1949: 346; 1969). His study *The Web of Kinship among the Tallensi* (1949) devoted considerable space to relations between parents and children, sibling relations, and domestic family arrangements. The separation which he himself had introduced between two domains of kinship could, however, be taken to imply that the social

> context in which the nuclear family was set – in other words, wider kinship arrangements – carried greater analytic significance. The politico-jural domain of kinship – public roles or offices ordered by wider kinship relations, and the political and religious aspects of kinship – were described analytically as a source of cohesion in the societies anthropologists studied, and hence what rendered kinship of interest for anthropology (see e.g. Radcliffe-Brown 1950).
>
> It is thus perhaps not surprising that the comparative study of kinship could devote relatively little attention to intimate domestic arrangements and the behaviour and emotions associated with them [note]. These were assumed to be to a large degree universally constant or a matter for psychological rather than anthropological study. If one considers Fortes' meticulous ethnography, it is quite paradoxical that the very data which documented in detail the small everyday acts of constructing relatedness between women, or between women and children, might be more or less excluded from the frame if his more general injunctions were taken seriously." (Carsten 2000, 17)[Carsten notes the exception of Goody's 1958 *The Developmental Cycle in Domestic Groups*]

Carsten's perspective is not unique. Overing and Passes (2000) introduce the studies in their recent volume as;

> "[D]irected at overcoming a prejudice inherent in Western political, legal, social and moral theory which separates the dominant 'domain of the public' (the cool and rational space of societal relationships which are ruled through contract and law) from the contingent 'domain of the domestic' (the hot and affective space of personal family relationships centred around the everyday care and responsibility of children)." (Overing & Passes 2000, 3)

They believe that this separation between 'public sphere' and 'domestic sphere' is inappropriately applied to Amazonian cultures;

> "To understand the difference between Western theory and the Amazonian vision and practice, the distinction must be made between collectivity as might be expressed through social-structural imperatives (through roles, statuses and juridical rules) and the collective *as an* attachment to (or among) the people who follow specific cultural and social ways of being. Many indigenous peoples of Amazonia are strongly, adamantly, fond of their own cultural and social ways of *doing* things, and

> of the people with whom they share them, but not of heavy imperatives of social structure or collectivity (cf. Overing 1999). Again, we need to find the paths into *their* sociality, and the one that we suggest to be followed pays closer attention to the ways and wherefores of Amazonian peoples' attachment to people: what for them are the conditions for human sociability?" (Overing & Passes 2000, 14, emphasis in original)

Stafford (2000) notes the significance of the 'two separate domains' model in traditional accounts of Chinese kinship, illustrating this by way of quoting from the 'seminal' work of Freedman;

> "We can show without much difficulty that kinship bound together large numbers of people in Chinese society and exerted an important effect on their political, economic, and religious conduct at large. Family is another matter. Essentially, its realm is that of domestic life, a realm of co-residence and the constant involvement in affairs of the hearth, children and marriage. Kinship is something different." (Freedman 1979, 240-241, quoted in Stafford 2000)

Stafford succinctly summarises the problem with such an approach, that; "this formalist approach is liable, I think, to obscure in anthropological accounts the lived experience of Chinese kinship…" (Stafford 2000, 37). Gow agrees; in Amazonia "Personal experience, as I discuss here, is also central to native people's understanding of kinship. Kinship is about relations between living people." (Gow 1991, 151). Similar points relating to Amazonia are also made by Vilaca (2002).

In contrast to the traditional accounts of 'kinship', we have seen how a renewed interest in everyday personal experience and interactions has influenced contemporary ethnographies (chapter 8). As suggested in the discussion by Overing and Passes (above) the concept of 'attachment' has sometimes proved useful. This point was made strongly by Stafford (2000a, see also chapter 1) who suggested that attachment theory's perspectives on social bonding could provide a useful base for anthropological accounts;

> "Might Bowlby's realist approach –… be a useful starting point for anthropologists? … One could make the case that *all* anthropological discussions of relatedness – e.g. the accounts by Malinowski, Mauss, and a great many others of the ways in which gift exchange and reciprocity, or commensality and the sharing of 'substance', help to constitute human

> relatedness – are also by definition, dealing with intractable problems of attachment and separation in social life." (Stafford 2000, 12, 24, emphasis in original)

Many of the accounts reviewed in chapter eight used concepts from attachment theory to describe social bonds. Marshall (1977) for example referred to *ttong* – 'feelings of strong sentimental attachment' which are demonstrated by nurturant acts. Other discussions are, like Stafford, more explicit in their reference to the potential utility of an attachment approach (e.g. Sault 1995, Lowe 2002). Lowe explains why he explicitly pursues an analysis guided by attachment perspectives;

> "This article examines the ways emergent human psychological needs and social identities dynamically intermingle through experience to organize meaningful social relationships. Specifically, I examine the idealized cultural models that associate kin-based identities and acts of need fulfilment and how these models mediate the formation of personally meaningful and socially legitimate relationships in Chuuk Lagoon (formally Truk) of the Federated States of Micronesia (FSM). My purposes in doing so are twofold. First I intend to contribute to a long-held – but often neglected – concern in anthropology with the contribution of human psychology to culture and social process in everyday experience (e.g. Hollan 2000; Malinowski 1930). Second, I hope to contribute to the recent efforts to overcome some of the stubborn theoretical divides in anthropology that separate the study of the psychological and social aspects of organized human relationships and systems of cultural meaning (e.g. Bourdieu and Wacquant 1992; Shore 1996)." (Lowe 2002, 123)

In reviewing Bowlby's discussions in chapter seven, I suggested that a weakness of traditional attachment theory, particularly applied to adult social bonding, is that most analyses are limited to social patterns prevalent in Western culture (see chapter 7). Lowe agrees with this;

> "It is now widely recognized that the qualities of emotional attachments to a variety of relational partners remain important for the adaptive negotiation of social relationships throughout one's life (Antonucci 1985; Herzberg et al. 1999; Levitt 1991; Levitt et al. 1994; Mikulincer and Florian 1999). While this point may be conceded by most, attachment-orientated research remains largely concerned with those attachment

> processes and resulting personal understandings that emerge from the earliest interactive experiences and relational partners, typically mothers and, occasionally, fathers. Few studies have examined the attachment processes and outcomes surrounding other relational dyads that develop later in the life course (Levitt 1991). Fewer still have examined cultural variations in the attachment processes across the life span." (Lowe 2002, 124)

Where traditional attachment studies have not been able to illuminate cultural variations in patterns of attachment and social bonding, increasingly, ethnographers are providing insights. Ainsworth's early study of infant attachment behaviour amongst the Ganda was an important exception here, as has been work such as that of Tronick et al. as discussed in chapter seven. Most attachment theory is however clearly based on data and studies from Western culture. Since it is by now clear that patterns of social bonding in Western culture are not representative of human societies in general, there is great opportunity for ethnographers to supply more detail to our understanding of the variables involved in attachment and social bonding.

9.3 MALINOWSKI AND THE PROCREATIVE VIEW

Before we move on to the summary of the current thesis let us remind ourselves of the opportunity for clarification that Schneider outlined on the basis of his review of anthropology's traditional perspective on social bonds. We have seen (chapter 8) that Malinowski argued forcefully that kinship is essentially about individual, sentiment-based social ties formed in childhood rather than being primarily some clan-based phenomenon. Richards also took this position. This position predates all current similar ethnographic emphases on the place of sentiments and attachments reviewed in chapter eight, as well as the focus discussed in previous section. But there is a key difference. From the post-Schneider perspective, the problem with these early accounts is that, in orientating around biological need fulfilment (and in Malinowski's case explicitly linking this to procreative function) they did not question the 'blood-ties' conception of 'kinship' and, arguably, reinforced it. Schneider gives an account of Malinowski's adherence to the traditional blood-ties concept;

> "Most important for the problem here is Malinowski's view that kinship consists of bonds which are essentially psychobiological in nature. Culture can bend them, but only so far, and not very far at that. Malinowski's view of adoption makes this clear;
> *Social and cultural influences always indorse and emphasize the original individuality of the biological fact. These influences are so strong that in the case of adoption they may override the biological tie and substitute a cultural one for it. But statistically speaking, the biological ties are almost invariably merely reinforced, redetermined, and remoulded by the cultural ones. (1930b: 137)*
> A note on adoption is in order. Malinowski says that adoption is a case in which culture is so strong that it overrides the biological tie and substitutes a cultural tie for it. If this were true it would present a problem, and seeing this, Malinowski suggests that it is really no problem at all because ties like adoption are rare; that is, "statistically speaking, the biological ties are almost invariably merely reinforced, redetermined, and remoulded by the cultural ones."
> The problem that Malinowski points to is this. If the blood relationship is presumed to have inherent qualities of its own which "are" and which "exist" and are so strong and take such precedence, then adoption ought not to be possible, or at most it should be unusual and rarely practiced." (Schneider 1984, 171-172)

Weismantel (1995, 688) makes a similar point; "But adoption, in which a consanguineal relationship is wholly fabricated, seemed so problematic that he [Malinowski] was driven to assert that is must be statistically uncommon (1930:137)". Schneider pursues this line of argument further;

> "For Malinowski the problem was to show in general the ways in which social kinship were determined by its vital psychobiological functions.
> In setting the biological aspects of kinship aside, there was felt no need to redefine kinship. It could still be defined as dealing with human reproduction as a social and cultural phenomenon. One could still assume that Blood is Thicker Than Water but not dwell on that part of it. Indeed for Malinowski and those who followed his sort of functionalism it was more convenient not to dwell on it, for to do so raised the whole question of precisely how specific social forms were constrained or determined by what particular biological conditions by what specific mechanisms, questions which they glossed over with glittering generalities." (Schneider 1984, 193)

Schneider's probing is right on target – not just for Malinowski and 'followers' within anthropology, but, perhaps even more so, for those sociobiologists and evolutionary psychologists (like Daly and Wilson) who overlook any investigation of mechanisms of social bonding. But in investigating the biological perspective on social bonding, and in focusing attention on the mechanisms by which social bonding occurs, some clarification is possible. Malinowski's reference to the *statistical relationship* between 'social kinship' and 'physical kinship' is particularly pertinent here.

In Malinowski's thinking, statistically, social kinship is somehow expected to follow physical kinship, because the biological fundamentals (procreation and the meeting of biological needs) are 'the basis' for the social relationship. In this case, as Schneider puts it, "adoption ought not to be possible, or at most it should be unusual and rarely practiced".

The dilemma Malinowski faced has been a common one for both anthropologists and sociobiologists since. This can be resolved with a distinction, always necessary in biological analyses of behaviour (Tinbergen 1951), between the evolutionarily typical statistical outcomes and selective forces involved in *the evolution* of characteristics, and the circumstances that mediate *the expression* of those characteristics. It is this distinction that the current thesis has attempted to highlight.

Malinowski's logic that social relationship 'should statistically' follow physical relationship in fact parallels biological theory's description of a necessary condition for *the evolution of* social behaviour. But, crucially, *not the expression of social behaviour.*

9.4 REVIEW AND SUMMARY OF THE STEPS OF THE THESIS

The review of the transitions in kinship theory conducted in chapter one demonstrated the potential value of any clarification of the relationship between 'the scientific facts of biology' and the social bonding behaviours of humans. I suggested that, following the growth of contrary ethnographic evidence and the theoretical work of Schneider (1984), the concept of a necessary fundamental association between genealogical ties and social bonds has been rejected by the majority of contemporary kinship theorists.

Nevertheless, for many social scientists, questions still remain about the relationship between biology and social bonding. For some (e.g. Goodenough 2001), the belief is that genealogical and procreative ties really are an underlying factor, but a clear demonstration of 'just how' is absent (Schneider 1984, see above section). For others (e.g. Carsten 2000, see chapter 1.7) the connection between social bonding and 'biology' is of a different kind, and notions of various processes of *nurture* creating social bonds and attachments have increasingly been part of ethnographic analyses and theoretical discussions.

Yet another current perspective, essentially continuous with sociobiological hypotheses stemming from the 1970s, is that there is indeed a natural association between genetic links and social bonds; it is claimed to be 'part of evolved human nature' to direct social behaviour towards genetic relatives (e.g. Daly et al. 1997). The evidence, as before (e.g. Sahlins 1976), shows this view to be wrong.

The 'scientific facts of biology' are reviewed in chapter two. The basic theoretical position, *inclusive fitness theory*, is a widely accepted description of a key aspect of the selection pressure that exists on the evolution of social behaviours. Hamilton's view was that the correct interpretation of inclusive fitness theory requires an understanding of Price's clarification about the statistical associations which natural selection acts upon (Price 1970). Price's work emphasised that the change in frequency of an hereditary characteristic depends on the statistical covariance between that character and reproductive fitness. Similarly, Hamilton (1970) showed that the inclusive fitness criterion describes the condition of statistical association between genotypes of actor and recipient necessary for the evolution of social behaviour (Frank 1995).

It was noted that 'the criterion' does not specify mechanisms for the expression of social behaviours beyond this requirement of statistically (in typical evolutionary environments) benefiting replica genes. It was also noted that the criterion describes one of the necessary conditions for the evolution of social behaviours, but that more primary necessary conditions exist.

I further argue that to understand whether social behaviours might evolve in a given species, and what forms these social behaviours might take, requires an analysis of the potential for and context of social interaction in the past evolutionarily typical environments of that species (Sherman 1980). We note, following Dawkins (1979) and Hamilton (1964), that the proximate expression of social behaviour that meets the criterion might be mediated by straightforward context-based rules of thumb. Since a reliable context of social grouping is a prior condition for the evolution of social traits treated by inclusive fitness theory, I argue that it is parsimonious that the proximate mechanisms should also be context-based.

With this solid and unelaborated interpretation of inclusive fitness theory set out, we were in a position to take a brief detour away from biological theory into a review some past popular interpretations of the theory in chapter three. In particular, we review early sociobiological hypotheses advanced by *Darwinian anthropology* to attempt to explain certain features of human kinship organisation. These sociobiological approaches had problems accounting for the ethnographic data and relied on a particular interpretation of inclusive fitness theory, which I (along with many biologists) suggested to be wrong. From the anthropological perspective, Darwinian anthropology treatments' focus on unilineal descent constructs was unfortunate, since most anthropological research had moved away from these perspectives by the late 1970s and 1980s. More importantly, they could not account for the data. From the biological perspective (but see also Schneider's critique of Malinowski above 9.3) these sociobiological approaches also ignored the whole issue of the proximate factors involved in the *expression* of social behaviours.

The critiques of Darwinian anthropology from within biology gave rise to the current evolutionary psychology school. In light of this, it is particularly surprising that, where evolutionary psychologists have returned to treatments of anthropological kinship data, they follow precisely in the footsteps of the Darwinian anthropologists (e.g. Daly et al. 1997). We also noted that, in an ironic twist, Daly et al., in support for their claim that humans everywhere culturally value actual blood relatedness, cited Schneider’s work which was in fact specifically about the (perhaps unique) prioritising of blood relationship in American culture.

At the close of chapter three we found that Kitcher, in his critique of the sociobiological position, suggested that the expression of social behaviours in humans might quite simply be based on cues of context and familiarity, rather than genetic relatedness *per se*.

In chapter four, spurred by the questions over of the proximate mechanisms of the expression of social behaviours, we returned to issues of the interpretation of inclusive fitness theory, in particular, what has come, perhaps unhelpfully, to be called ‘kin recognition theory’. We noted a few important distinctions which need to be observed in this area. Social behaviour statistically benefiting replica genes (often via genetic relatives) in the species’ normal (evolutionarily typical) environments strictly requires only that a form of what some have called ‘kin discrimination’ is typically the outcome of the behaviour. Kin *recognition per se* is thus not actually necessary, and not strictly *predicted* by inclusive fitness theory. Thus, for any given behaviour, what effectively amounts to ‘kin discrimination’ might come about via ‘location-based’ or ‘context-based’ cues that have reliably correlated with genetic relatedness in evolutionarily-typical environments, or might also/alternatively come about via ‘positive powers’ of *recognition* of genetic relatedness based on a mechanism such as self-referent phenotype matching.

However, even if an organism demonstrates an ability to distinguish genetic relatives from non-relatives, this must be interpreted cautiously. Other than social behaviours, inbreeding avoidance can be a selective force upon an ability to make this distinction, and thus the discrimination may have nothing to do with the mediation of social behaviours. Further, what may apparently be self-referent phenotype matching observable under laboratory conditions might in fact be a side-product of what would usually be a mechanism for learning phenotypes in a social context of *likely* genetic relatives for ‘other-referent phenotype matching’ under natural conditions (e.g. Sherman et al. 1997).

Having outlined the theoretical position in chapter four, we review the evidence relevant to mammal species in the following chapter. Given the importance of knowledge of the typical social context a behaviour is expressed within, we first look at how a species' ecology and niche fundamentally influence its demographics, and the potential for interactions between individuals. We note that a basic characteristic of most mammals is the typical reliability of the context of interaction between a female and her infant offspring, who are very often isolated from other individuals. A related point to note is that contexts of interaction will differ significantly for different kinds of genetic relatives, even relatives of the same degree (or magnitude) of genetic relatedness. One example is the context of interaction between maternal half-siblings who are likely to interact with each other and the mother in the nursing context, and on the other hand, paternal half-siblings, who are neither likely to encounter each other, nor necessarily interact with the genetic father in most mammals.

The evidence on the expression of social behaviours in mammals demonstrates that context-based behavioural discriminations occur in the great majority of species studied. Although there is some evidence that a type of self-referent phenotype matching appears to operate in a small number of species (two mammal species according to Hauber and Sherman 2001), the role of context, and particularly the place of social familiarity appears crucial even where some positive powers appear to be present. We note that in species with behaviours such as male infanticide, selection would not favour signalling of actual genetic 'identity' (e.g. Pagel 1997, Sherman et al. 1997). We also find that for the expression of social behaviours to be mediated by familiarity requires the social learning of individual identities as well as behavioural biases towards these individuals. The concept of social bonding encapsulates these two effects, and is widely used in the study of mammal social behaviours (e.g. Gubernick 1981, Walters 1987).

We close chapter five by consolidating the crucial distinction between the expression of social behaviours and the evolution of social behaviours. This distinction allows us a clear perspective on the scope of Hamilton's inclusive fitness theory. The latter specifies a criterion (a statistical association involving identical genes) which is a necessary condition for *the* *evolution* of certain kinds of social behaviours. It is erroneous to interpret it as specifying a sufficient condition, since an *ecological potential* that provides scope for social interaction is a more fundamental necessary condition.

On the other hand, for *the expression* of social behaviours, genetic relatedness is neither a sufficient nor even a necessary condition. Mediating circumstances that would, in evolutionarily-typical conditions, reliably statistically correlate with genetic relatedness, are a sufficient condition for the expression of social behaviours. This distinction between *evolutionary* process and the *expression* of behaviour clarifies how the concept of genetic relatedness plays a role in biological theory of social behaviour.

I argue that applying biological theory to an understanding of social bonding and the expression of behaviours in humans requires an understanding of evolutionarily typical environments, just as for other mammals. An analysis of the basic ecological and demographic features common to closely related primates, and particularly African apes, (in addition to the insights gained into common features of mammalian demographics) is thus required. Chapter six reviews the evidence. We find that, like other mammals, *Catarrhini* primate demographics are strongly influenced by ecological conditions, particularly density and distribution of food sources. These species have low birth rates and long periods of infant dependency, particularly so in African apes. Cohesive social groups and delayed natal dispersal mean that maternally related individuals, including maternal siblings, face a statistically reliable context of interaction in all *Catarrhini* primates. This reliable context of interaction with maternally related individuals is extended amongst those species with female philopatry (especially *Cercopithecinae*).

In reviewing evidence on what mediates social behaviours in primates, we find similarity with other mammals; that social context based cues are overwhelmingly important. Social behaviours between potentially paternally related individuals are generally less marked than between maternal relatives in primates. Nevertheless, where such interaction does occur, there is abundant evidence from numerous sources that male interaction with potential infants is mediated via familiarity with the female caring for the infant. Social interactions between potential paternal siblings are also mediated by social context, because in most species, paternal siblings, in those cases where they are present, are likely to be members of an individual's peer group. There is evidence that some positive powers may accompany these circumstantial cues mediating paternal sibling interaction, but the latter are found to be more crucial, which makes sense considering that paternal siblings may often not in fact be present, but social interaction with peers is nonetheless likely to still be individually beneficial.

For maternal relatives the evidence strongly points to circumstantial cues mediating social bonding and social behaviour. Adoption of infants by females (and sometimes males) demonstrates that caregiving and bonding to infants is not mediated by positive powers of discrimination. From the infant's perspective, it will bond with any responsive carer. If not necessarily the actual mother, in natural conditions this will often be a maternal relative (particularly an older sibling), but the context is primary, not the actual relatedness. Similarly, social bonding and social behaviours between maternal siblings (and occasionally between other maternal relatives) is context-driven in primates, and mediated via the caregiver.

Confirming the value of considering primate demographics and social bonding mechanisms, in chapter seven we find that the area of study most closely concerned with mechanisms of social bonding in humans considers there to be continuity between humans and other primates in the operation of these behaviours. Ethological attachment theory, largely devised by Bowlby and colleagues in the second half of the twentieth century has investigated mechanisms of social and emotional bonding in humans, particularly the attachment bonds of infants to their caregivers. In support of the interpretation of inclusive fitness theory set out in this thesis, Bowlby (1982) himself stated that the evolution of social bonding that typically occurs between an infant and its carer should be understood in terms of this biological theory.

Bowlby demonstrated the primate-typical nature of basic human social bonding mechanisms. His work demonstrated that social attachments form on the basis of provision of care, and responsiveness to elicitations for care. The social context of living together and the familiarity this brings, provides the circumstance within which social bonds can form. However, we noted that some of Bowlby's descriptions of the 'normal' patterns of ties that develop in humans depended on a perspective on 'normal' living arrangements perhaps biased towards Western cultures, and that the identities of bonding figures might be different under alternative arrangements. We particularly noted a lack of recognition of the frequency of care-taking by older-sibling figures in many societies. In attempting to define more specific forms of *the giving of care and nurture* which may mediate social bonding we found that provision of food is likely to play a part, as well as the more intangible provision of warmth and comfort, and a safe base for sleeping.

Having derived these basic mechanisms of social bonding from attachment studies, as well as insights gained from the reviews of social bonding mechanisms observed in primates and mammals, chapter eight found us in a position to compare what are usually understood to be very different perspectives on social bonding. On the one hand are the perspectives from theoretical biology and attachment studies, and on the other, anthropological treatments of social bonding and ethnographic reports describing processes and conceptions of social bonding in various cultures. Is there compatibility between these perspectives?

In chapter eight we found that Robertson Smith had noted the importance of sharing food in creating social ties, although his analysis excluded the context of childcare and focused on bonds between 'kinsmen'. Richards, under Malinowski's influence, refocused on the importance of food meeting 'the needs of the infant', and food provision mediating social bonds, (although she maintained the association with the procreative relationship). Alternative ways of considering the basis for social bonding emerged later, particularly after clear evidence - that living together mediates 'becoming kin' - had emerged from the New Guinea highlands, and various theoretical critiques questioned the genealogical perspective (culminating in Schneider's 1984 critique as discussed in chapter 1).

Ethnographic accounts focusing on the processes mediating social bonds emerged in the 1970s. For example, Witherspoon (1975) reported that all social bonding in Navajo society, not just that between the infant and its carer, is based on giving and sharing of loving care and sustenance. Other ethnographies demonstrate that bonds first formed during childhood often remain important throughout the lifespan (e.g. Gow 1991). Throughout the review we found that many contemporary accounts focus on social bonds formed in childhood and the importance of the performance of acts of care, including food provision, in mediating these bonds. In all cases it is this performance of care which is considered the overriding factor in mediating social bonds, notwithstanding 'blood ties'. In short, there is strong compatibility between the perspectives on social bonding that emerge from a proper account of biological theory and those documented by ethnographers.

9.5 INTERPRETING BIOLOGICAL THEORY - SUMMARY

In terms of theoretical orientation, the current thesis interprets basic biological theory significantly differently from the interpretations common to sociobiological and evolutionary psychological accounts. I argue that inclusive fitness theory describes one necessary condition or 'criterion' for the increase in frequency (evolution) of certain kinds of social behaviour traits (as defined in chapter 2). This condition concerns the statistical covariance of identical genes between actor and recipients of such social behaviour. Being a theory about selection pressure on traits, the condition is relevant to typical outcomes in evolutionarily typical environments – statistical outcomes are key.

Inclusive fitness is commonly incorrectly referred to as something like a formal proof that organisms *will always engage in social behaviours with genetic relatives*. That is, it is interpreted not only as an evolutionary-level explanation, but as a proximate-level theory *and even prediction* governing the expression of individuals' social behaviour; and as justification for the claim that *organisms have evolved to* direct social behaviour towards genetic relatives. This is absolutely wrong, and the basis of a great deal of error.

Another important feature of the interpretation of inclusive fitness theory I am arguing for is that it specifies a criterion; *one necessary condition*, but not the most primary necessary condition for the evolution of social behaviours. This point is also strongly underemphasized in typical discussions. Sherman (1980) gives a clear account of the fact that demographic potential must exist for a context of interaction before any behaviour describable as 'social' can occur. As Hamilton (1987) puts it; "in this sense social behaviours are conditional from the start."

In overlooking the prior necessary condition dictated by ecological potential, and in combination with misunderstanding the distinction between evolutionary/proximate explanations, many accounts of inclusive fitness theory suggests that individuals *will express social behaviour towards genetic relatives*, and point to 'Hamilton's rule' (about the trade-off between cost/benefit and degree of relatedness, see chapter 2) as the only relevant condition. This interpretation completely ignores the ultimate/proximate distinction, and the place of evolutionarily typical demographic patterns and contexts of interaction, and can make no sense of, for example, sibling cannibalism (as described in chapter 4) where it occurs.

There are further implications of these fundamental misunderstandings. Overlooking the point that a reliable context of interaction is a prior necessary condition for the evolution of social behaviours obscures the fact that context-based cues will therefore usually be available for mediating the expression of social behaviours. Context-based cues should thus provide us with a parsimonious starting position for investigating such proximate mechanisms. In chapter four, we found that even the name "kin recognition theory" gives an (incorrect) impression that some kind of 'active recognition' of genetic relatedness is *expected* to mediate the expression of social behaviours. This point is also made by Grafen (1991) and Tang-Martinez (2001). All the evidence suggests that 'the criterion' has been met by context-based social bonding and behaviours in the vast majority of mammal species studied, not by 'active recognition'.

A crucial implication of this argument taken as a whole is that *the expression of the kinds of social behaviours treated by inclusive fitness theory does not require genetic relatedness*. Sociobiology and evolutionary psychology's claims that biological science predicts that organisms *will* direct social behaviour towards relatives are thus both *theoretically* and *empirically* erroneous. Such claims and their supporting arguments also give a highly misleading and reductive account of basic biological theory. Properly interpreted, *cultural anthropology approaches (and ethnographic data) and biological approaches are perfectly compatible* regarding processes of social bonding in humans. Most of all, this requires a focus on the circumstances and processes which lead to social bonding.

9.6 CORRELATION BETWEEN CORESIDENCE AND GENEALOGY IN EURO-AMERICAN SOCIETY

Schneider documented the prevalence of the 'blood is thicker than water' view at the heart of traditional anthropological perspectives on social bonding for over a century, and suggested that this was derived from values prevalent in anthropologists' own cultures (Schneider 1968, 1984). I want to briefly look at how this feature of Euro-American culture may be influenced by genealogy and coresidence *correlations* and that apparent correlation may be confused for root cause. Murdock's summary of residence patterns is suggestive;

> "Neolocal residence isolates [the individual] before marriage with his family of orientation and thereafter with his family of procreation… The development of neolocal residence, in societies following other rules appears to be favoured by any influence which tends to isolate or to emphasise the individual or the nuclear family… Individualism in its various manifestations, e.g., private property, individual enterprise in the economic sphere, or personal freedom in the choice of marital partners, facilitates the establishment of independent households by married couples. A similar effect may be produced by overpopulation and other factors which stimulate individual migration, or by pioneer life in the occupation of new territory, or by the expansion of trade and industry, or by developing urbanization. A modification of inheritance rules, such as the replacement of primogeniture by the division of an estate among a number of heirs, can likewise favor neolocal residence." (Murdock 1949, 202-204)

Murdock is not alone in making these suggestions. Some similar points are visible in Macgregor (1946; see Cohen's 1961 summary below 9.8). Firth (1956) also makes some similar observations, in this case specifically about Western society, particularly noting that this relative isolation may not be limited to urban environments;

> "The general patterns of industrial living have penetrated modern Western rural society far further than is often thought. For instance, in a

> remote Dorset village, a young man who had grown up there, but been away for a while, said rather ruefully that he did not know the people who were living two doors from him. Even in a country village the neighbour relations have far more of the impersonal quality often attributed solely to urban living than is commonly realised. I have referred to such a hypothesis, even though it may be unacceptable, in order to emphasise the relation between nearness or separation of residence and maintenance or obliteration of kin relations. Any investigation of kinship in an urban environment soon brings out the great degree of variation in relations with kin. The reasons for this are complex, and their force in various types of kin situation is not entirely clear. But among the correlates of the varying recognition and maintenance of kin ties would appear to be the following; residential accessibility; common economic interests, as in occupation, or in property-holding; composition of household; composition of elementary family, especially as regards that of the sibling group…" (Firth 1971 [1956], 389)

Many sections of Euro-American societies have been marked by demographic factors leading to individual isolation, and in these conditions, particularly where combined with shifting, temporary residence (e.g. due to the necessity of labour mobility), contexts of repeated social interaction are often limited to the household itself. With neolocal residence, as Murdock notes (see also Bowlby chapter 7), household is typically comprised of other members of a 'nuclear family', either parents and siblings, or spouse and children. This concept of 'nuclear family' appears to beg the question of the relationship between social and physical kinship, but if monogamous spouses live together in isolation after marriage separated from additional interaction contexts that would normally mediate social bonds and 'create kinship', such social bonds would rarely develop. Under the system Murdock describes, the one reliable class of individuals who could typically enter into this minimal community of the spousal household would be the couple's (typically biological) offspring. The repetition of this pattern over a few generations would soon lead to a situation where social kinship independent of genealogical relationship is rare (fostering/adoption) or non-existent and genealogical links and social bonds are *de facto* highly correlated. The pervasiveness of this correlation may exert an influence on cultural conceptions of the 'naturalness' of the association between genealogical ties and social bonds, without the basis of the correlation which leads to this generalisation being clearly recognised.

In a society where social bonds are culturally conceived to be 'naturally' associated with procreation and biological relationship, anthropologists unpractised in reflexivity may also project this conception onto other cultures, and overlook variations and alternative influences. This is what Schneider argued to be the case, and why he emphasised that the basis of this conception needs to be examined and justified, rather than referred to in vague terms and, as he put it, "glossed over with glittering generalities" (see above 9.3).

9.7 BUT ONE OF THE CONDITIONS TO WHICH KINSHIP SYSTEMS MUST ADAPT

We have noted above and in chapter one that Schneider didn't reject the idea that social bonding might have some connection to the 'scientific facts of biology'. The current thesis has suggested a way in which this connection might be understood. However, Schneider's broader point was that constraining analyses of 'kinship' with reference to genealogical ties potentially obscures alternative insights. His main concern was the submergence of local culturally specific conceptualisations of social bonds and the processes that constitute them. But Schneider was also concerned about what other factors might be influencing patterns of social relationships. These other, submerged conditions which contribute to social patterns might be seen more clearly once assumptions about genealogy are put to one side;

> "If certain aspects of kinship could indeed be accounted for by the "ineluctable biological facts," while certain others could not, the question would arise as to the relation between them. Are those parts of the kinship system which are determined by the biological facts in some sense primary, while others are secondary and derivative? If, as Spiro says, "kinship systems must adapt to and are conditioned by variations in ecology, economy, demography, politics, and so on," do the biological facts have some priority or are they but one of the conditions, like ecology, economy, demography, etc., to which kinship systems must adapt? Take note: if the latter is the case, then kinship must be as much rooted in these other conditions as in the biological facts." (Schneider 1984, 139)

The above discussion of some of the conditions that may have led to the isolation of nuclear families in Western society is consistent with the idea that social bonding patterns are influenced by economy and demography. More generally, broad agreement about the ways in which social bonds tend to form might provide a good platform for studies of social change. In the remainder of this chapter, I want to draw on ethnographies from a range of societies, from East Asia to North and South America, to illustrate how multiple conditions influence social patterns.

We start with Stafford's discussion of the various influences on social patterns in Chinese culture, which demonstrates that even official patrilineal kinship is in reality fluid and moulded by various forces;

> "Without question, in many Chinese contexts ties based on mutual assistance, coresidence, friendship, and discipleship may be more significant than ties of kinship.
>
> Historians and anthropologists have also shown that Chinese patriliny only ever operates in a wider politico-economic context (see e.g. Gates 1996). That is, they have problematised the notion of pan-Chinese timeless principles of kinship, and shown that descent, as such, never 'stands alone'. The volume edited by Faure and Siu (1995) addresses, among other things, the mutual impact of ethnicity, state-building, and lineage development in a single Chinese region, suggesting that the political economy of land control, and considerations of ethnic differentiation, may be as significant in lineage development as considerations of kinship in the narrow sense. Rubie Watson (1985) examines the interrelation of patrilineal ideology and class, and shows how patriliny may underpin class exploitation within lineages. The volume edited by Davis and Harrel (1993) analyses the (often paradoxical) impact of state intervention and official ideology on kinship practice in post-Mao China. In short, in terms of Chinese history, and even within the history of Chinese kinship, ethnicity, class, and state intervention must be viewed as equal players with 'patriliny.'" (Stafford 2000, 50)

Another case where history and state intervention has affected social arrangements and the strength of bonds is amongst the Teton Dakota of North America. Originally this society followed an open social structure, which Macgregor (below) refers to as bands. This changed considerably after land reforms were introduced by the government. These produced economic and residential conditions that resembled those established in mainstream North American society. Macgregor shows how these had crucial consequences for basic social patterns;

> “*“Occasionally the band included other families who joined either to escape some unpleasant social pressure or to become the followers of some renowned warrior. There were also larger bands of related and unrelated extended families, which maintained social unity the year round”*… Generosity, one of the most highly esteemed values in Teton Dakota life, was the principle basis of the system of food distribution. Open-handedness was not only a cardinal criterion of behaviour among kinsmen, but was extended to unrelated members…
>
> Since their “pacification” and settlement on the reservation, changes have occurred in the structuralizations of relationships among many of the Teton Dakotas with concomitant shifts in the system of distribution. Aside from the loss of the buffalo as the source of subsistence, and of warfare as the primary source of prestige, perhaps the most significant change which transpired among the Teton Dakotas was the loss of the ancient band organization and the dispersal of individual households. As a result of the American system of land allotments to individual families, individual extended families are *“stretched in a line of separated homes.” “Family homes are geographically widely separated today in comparison with the band camp”;* as a result, “*the family now lives with greater independence of related families in its own farm home.”*
>
> Concomitantly, significant changes from these shifts can be observed on many levels, not only are the *“associations within an extended group… less frequent and intensive,”* but energies which were formerly directed outside the family are now turned into it.
>
> “*The mother’s role has also gained by the present isolation of the individual household. Formerly the family lived in a camp with several other related families, with whom the child associated freely. Now the child living in a farmhouse on an allotment is forced to spend much more time with his own family and especially with his mother.”*
>
> In line with the status of the family as a productive unit, *“the individual and the individual family can, if they so desire, support themselves on a farm or by wage work without the assistance of others and can find companionship and social life outside the community.”*” (Macgregor 1946, in Cohen 1961 [1955], 344-345)

These changes in social bonding patterns mark a submergence of the Teton’s long-standing social organisation and the shift to a way of life typical of wider U.S. culture. Schrauwers (1999) also discusses the affect on social relationships of the imposition of resettlement policy and a change in subsistence economy on the people of central Sulawesi, Indonesia. This has a profound affect on patterns of social relations between siblings;

> “While the general outlines of official kinship have remained the same over the last century, the practical implications of these relationships have changed as economic and social conditions altered radically under Dutch colonialism. Subsequent to Kruyt’s pioneering field work at the turn of the century, the swiddeners now designated as the To Pamona have been reconstituted as a peasantry. They were resettled by the Dutch from hilltop hamlets in 1908 and forced to adopt wet-rice agriculture in the valley floor on the shores of lake Poso. This change in agricultural technologies involved fundamental changes in relations of production through the introduction of individually owned landed property, the market, and wage relations. Following Kahn (1993), I refer to these changes as “peasantization,” a process with two major thrusts. On the one hand, this introduction of individually owned landed property resulted in a differentiation over time into viable and nonviable peasant households. Geertz (1963:97), in a different ethnographic context, described a similarly poor area as divided into “just enoughs” and “not quite enoughs.” On the other hand, peasantization means low capitalization, such that even viable households with sufficient property depend on so-called free (i.e. non-commodified) domestic labor to meet the bulk of their labor needs…
>
> Most smallholders acquire their land through inheritance, usually at marriage. Ideally parental holdings are divided equally among their children; however, as parental holdings have shrunk over the generations, many newly married couples have inherited too little to become viable households. Frequently older children will *magagu* (take more than their share) so as to reach that threshold of viability… practical kinship ties the viable households of older siblings (tukaka) to the nonviable households of their younger siblings (tua’i). Elsewhere I have noted the blurred household boundaries typical of sibling sets in contexts where non-viable households transfer some of their domestic functions to the more viable households of kin (Schrauwers 1995). One of these domestic functions is child rearing: unable to care for their children, they may ask their kinsmen with viable households to foster them. These kinsmen, still largely dependent on domestic labor for the cultivation of their fields, may actively seek to foster older children (both boys and girls) for the contribution they can make in reducing the household’s dependence on wage labor…
>
> The domestic exploitation which occurs within the kinship sphere is thus crucial to maintaining the viability of peasant enterprises. This

> exploitation, however, is not a simple perpetuation of historical relations of servitude but a form of labor mobilization that has emerged in the niches of the capitalist transformation of the highlands. The so-called free labor of kin is a substitute for wage labor, peasant producers cannot afford wage labor because so much of their own surpluses have been drained away by the mengijon [agricultural loans] system. Green revolution inputs such as improved irrigation, fertilizers, and the mechanization of agricultural production have subordinated even viable subsistence households to the market since their access to these inputs is through the village merchants. The benefits of the green revolution thus accrue to the merchants, leaving peasant enterprises (including those of the bagagu) undercapitalised and dependent on noncommodified inputs." (Schrauwers 1999, 316-320)

Schrauwers thus demonstrates that changed subsistence options in an imposed environment of commoditisation of agriculture and a global economy can result in disruption to traditional relationships, even between siblings, as well as changed social and power relations between them.

Nuttall's work on the Kangersuatsiarmiit also describes the impact of economic change. He describes how global economic forces change patterns of social bonding within Inuit communities in Greenland. In particular, Nuttall describes the shift away from communal organisation towards economic individualism;

> "Like many other hunting societies, the Kangersuatsiarmiit do not only regard the environment as 'giving': sharing the products of the hunt is a social event that demonstrates relatedness, affection and concern. Cultural identity is founded upon and derives meaning from a culturally embedded system of sharing relations. As with many other Inuit communities that depend on hunting (see for example, Wenzel 1991), when meat is shared and exchanged in Kangersuatsiaq it is done so on the understanding that hunters have an obligation to distribute much of what they catch. This obligation to share underlies the customary ideology of subsistence in Kangersuatsiaq and contributes to the reproduction of kinship ties and other close social relationships. While this obligation to share remains strong, as I discuss below, there is an increasing commoditisation of hunting and some hunters prefer to try to sell meat…
>
> The sale of whale meat and other Greenlandic food, such as seal and fish, is being encouraged by the Greenlandic Home Rule government, although

> on a larger scale than the local-level economy… As well as other goods, Greenland relies to a great extent on imported foodstuffs, mainly from Denmark. To ease this reliance, hunters in small settlements such as Kangersuatsiaq are being encouraged to sell part or most of what they catch to Royal Greenland, the country's meat and fish processing and marketing company, rather than to share or sell the meat within the village… In many parts of Greenland, however, there is local opposition, or reluctance, to sell seal and whale meat to the Royal Greenland processing plants that are to be found in many villages… Royal Greenland has failed to recognise the essence of sharing as a fundamental part of the hunting culture, as well as understanding the immediate gains for a hunter who sells meat privately rather than to the Royal Greenland processing plant (Nuttall 1998b). Any meat that is sold is surplus and the money earned is essential for the economic viability of the hunter's household. Although some hunters do see the incentive to earn money as overriding other concerns such as sharing, for the most part when hunting is done to satisfy a market demand beyond the local community or regional economy, then the customary ideology of subsistence and notions of sharing and giving are disrupted and threatened…
>
> While I have argued that kinship does not determine or control the social organisation of commodity production, the ideology of subsistence and sharing sustains, renews and brings into being kinship relations. Kinship has certain dividends and entails moral obligation, and people choose, and wish to sustain, the relations they see as rich and meaningful to them. Now that the incentive for economic production in modern Greenland is increasingly market-driven, rather than framed by kinship, economic gain makes for social loss." (Nuttall 2000, 55-58)

Nuttall's account demonstrates how national and even international economic factors can impact social bonds at the local level. We have seen how such changes in local social patterns can lead to isolation of individuals in minimal social environments such as the 'nuclear family', and thus fundamentally alter norms of social bonding patterns in a society, and ultimately, cultural conceptions of social bonding.

Another form of outside influence on a culture's social bonding norms is via direct interaction between different cultures and the accompanying diffusion of concepts, symbols and practices. Weismantel illustrates this in describing the interplay between a Westernised view of social bonding, where 'real kinship' is founded on blood ties, and an indigenous Ecuadorian view of social bonds, as formed by processes of nurture. She describes an interaction between a man who is caring for a young child and a district nurse on a social call. Weismantel describes the nurse as "a young woman from Quito assigned to the parish for a year of "rural service" required by the government of all health professionals" who is "utterly out of place in the indigenous culture of the parish." She describes the interaction;

> "The man served the child hot soup, and sat back beaming, happily watching him empty the bowl. "He was an orphan, a poor boy, so I brought him here to live with me as my son," he explained. "Where he was living, there wasn't enough to eat."
> The nurse was horrified; she gestured to him frantically to lower his voice. "Don't talk like that in front of the boy," she whispered. "He's very young; maybe, if he's lucky, he'll forget about his own parents and grow up believing you're his real father." Iza, puzzled and offended, responding by raising his voice instead of lowering it. "I *am* going to be his father," he said irritably. "Aren't I feeding him right now?"
> The nurse's urgent need to hide the fact of adoption is based upon the assumption that in the absence of a "blood" tie, the relationship between man and child is fundamentally a pretense. The family as she envisions it is both biological and social in origin. If biological reproduction takes place outside of the social bond of marriage, an illegitimate child is the result: a "natural" son. But with Iza's attempt to establish a bond with a child whose mother he did not impregnate, it is the parent who becomes illegitimate: in the nurse's eyes, Iza could never be the "real" father of this child…
> From an indigenous perspective, insistence on the primacy of biological kinship is one of a large set of beliefs and practices that governmental and religious workers attempt to impose on local people. The bourgeoisie find fault with the indigenous and Afro-Ecuadorian cultural traditions for failing to delimit the nuclear family, a failing they characterize as an impediment to development and an indication of a fundamental incompatibility with modernity." (Weismantel 1995, 690)

Weismantel's analysis returns us to Schneider's central point. Constructing from narrow cultural particulars (Euro-American or otherwise) an essentialised model of 'human nature' does not constitute science; it is closer to cultural colonialism. In any analysis intended to shed light on proposed universals of the human condition, reflexivity is essential, and cultural and biological approaches both surely necessary.

REFERENCES:

Ainsworth, M. 1963. The development of infant-mother interaction among the Ganda. In *Determinants of Infant Behavior*, edited by B. M. Foss. New York: Wiley.

———. 1989. Attachments Beyond Infancy. *American Psychologist* 44 (4):709-716.

Ainsworth, M.D., and J. Bowlby. 1991. An ethological approach to personality development. *American Psychologist* 46 (4):333-341.

Alberts, S. C. 1999. Paternal kin discrimination in wild baboons. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266 (1427):1501-1506.

Alberts, S. C., and J. Altmann. 1995. Balancing Costs and Opportunities - Dispersal in Male Baboons. *American Naturalist* 145 (2):279-306.

Alexander, R. D. 1991. Social-Learning and Kin Recognition - Reply. *Ethology and Sociobiology* 12 (5):387-399.

Alexander, Richard D. 1974. The Evolution of Social Behavior. *Annual Review of Ecology and Systematics* 5:325-383.

———. 1979. *Darwinism and Human Affairs*. Seattle: University of Washington Press.

Altmann, J. 1979. Age Cohorts as paternal sibships. *Behavioral Ecology and Sociobiology* 6:161-164.

Altmann, S.A. 1979. Altruistic behavior: the fallacy of kin redeployment. *Animal Behaviour* 27:958-959.

Andelman, Sandy J. 1986. Ecological and Social Determinants of Cercopithecine Mating Patterns. In *Social Evolution in Birds and Mammals*, edited by R. W. Wrangham and D. I. Rubenstein.

Archer, John, and Barbara Lloyd. 2002. *Sex and Gender 2nd Ed.* Cambridge: CUP

Barbosa, D. 1866 (1500). East Africa and Malabar, edited by H. E. J. Stanley.

Barnes, J.A. 1955. Kinship. In *Encyclopaedia Britannica*. London: Encyclopaedia Britannica.

———. 1962. African models in the New Guinea Highlands. *Man* 62:5-9.

Barry, H., and LM Paxson. 1971. Infancy and early childhood: cross-cultural codes 2. *Ethnology* 10:466-508.

Batson, C.D., and L.L. Shaw. 1991. Evidence for Altruism: Towards a Pluralism of Prosocial Motives. *Psychological Inquiry* 2 (2):107-122.

Bekoff, M. 1981. Mammalian Sibling Interactions: Genes, Facilitative Environments, and the Coefficient of Familiarity. In *Parental Care in Mammals*, edited by D. J. Gubernick and Klopfer. New York: Plenum.

Belichon, S., J. Clobert, and M. Massot. 1996. Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecologica-International Journal of Ecology* 17 (6):503-517.

Belsky, Jay, Michael Rovine, and Margaret Fish. 1989. The Developing Family System. In *Systems and Development: The Minnesota Symposia on Child Psychology*, edited by M. R. Gunnar and E. Thelen. Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Berman, William H., and Michael B. Sperling. 1994. The Structure and Function of Adult Attachment. In *Attachment in Adults: Clinical and Developmental Perspectives*, edited by M. B. Sperling and W. H. Berman. New York: The Guilford Press.

Bernstein, I. S. 1999. Kinship and the Behaviour of Nonhuman Primates. In *The Nonhuman Primates*, edited by P. Dolhinow and A. Fuentes. New York: Mayfield.

Bernstein, I.S. 1991. The correlation between kinship and behaviour in non-human primates. In *Kin Recognition*, edited by P. G. Hepper. Cambridge: CUP.

Betzig, Laura L. 1997. Preface. In *Human nature : a critical reader*, edited by L. L. Betzig. New York: OUP.

Blatrix, R., and P. Jaisson. 2002. Absence of kin discrimination in a ponerine ant. *Animal Behaviour* 64:261-268.

Blaustein, A. R. 1983. Kin Recognition Mechanisms - Phenotypic Matching or Recognition Alleles. *American Naturalist* 121 (5):749-754.

Blaustein, A. R., M. Bekoff, J. A. Byers, and T. J. Daniels. 1991. Kin Recognition in Vertebrates - What Do We Really Know About Adaptive Value. *Animal Behaviour* 41:1079-1083.

Bloch, Maurice, and Dan Sperber. 2002. Kinship and evolved psychological dispositions - The mother's brother controversy reconsidered. *Current Anthropology* 42 (5):723-748.

Boas, Franz. 1911. *The mind of Primitive Man*. New York: Macmillan.

Bodenhorn, Barbara. 2000. 'He used to be my relative': exploring the bases of relatedness among Inupiat of northern Alaska. In *Cultures of Relatedness: New approaches to the study of Kinship*, edited by J. Carsten. Cambridge: CUP.

Bollinger, E. K., S. J. Harper, and G. W. Barrett. 1993. Inbreeding Avoidance Increases Dispersal Movements of the Meadow Vole. *Ecology* 74 (4):1153-1156.

Boots, M. 2000. Kinship and cannibalism in the Indian meal moth, Plodia interpunctella: No evidence of kin discrimination. *Evolutionary Ecology Research* 2 (2):251-256.

Borries, C., Launhardt, K., Epplen, C., Epplen, J. T., & Winkler, P. 1999. Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups–defence pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology* 46(5): 350-356.

Bouquet, Mary. 1993. *Reclaiming English kinship: Portuguese refractions of British kinship theory*. Manchester: Manchester University Press.

Bowlby, J. 1958. The nature of the child's tie to his mother. *International Journal of Psycho-Analysis* 39:350-373.

———. 1979. *The making and breaking of affectional bonds*. London: Tavistock.

Bowlby, John. 1969. *Attachment and Loss*. Vol. 1. London: Hogarth.

———. 1982. *Attachment, 2nd edition*. Vol. 1. London: Hogarth.

Bradbury, J.W., and S.L. Vehrencamp. 1977. Social organization and foraging in Emballonurid bats. III. Mating systems. *Behavioral Ecology and Sociobiology* 2:1-17.

Brady, Ivan A. 1976. *Transactions in kinship : adoption and fosterage in Oceania*. Honolulu: University Press of Hawaii.

Broude, G.J. 1994. *Marriage Family and Relationships*. Oxford: ABC-Clio.

Busse, Curt D. 1985. Paternity Recognition in Multi-male Primate Groups. *American Zoologist* 25:873-881.

Byers, J. A., and M. Bekoff. 1991. Development, the Conveniently Forgotten Variable in True Kin Recognition. *Animal Behaviour* 41:1088-1090.

Carnelley, K. B., P. R. Pietromonaco, and K. Jaffe. 1996. Attachment, caregiving, and relationship functioning in couples: Effects of self and partner. *Personal Relationships* 3 (3):257-277.

Carpenter, B. D. 2001. Attachment bonds between adult daughters and their older mothers: Associations with contemporary caregiving. *Journals of Gerontology Series B-Psychological Sciences and Social Sciences* 56 (5):P257-P266.

Carreno, C. A., T. J. Vess, and R. N. Harris. 1996. An investigation of kin recognition abilities in larval four- toed salamanders, Hemidactylium scutatum (Caudata: Plethodontidae). *Herpetologica* 52 (3):293-300.

Carrithers, Michael. 1996. Nature and Culture. In *Encyclopedia of social and cultural anthropology*, edited by A. Barnard and J. Spencer. London: Routledge.

Carsten, J. 2001. Substantivism, Antisubstantivism, and Anti-antisubstantivism. In *Relative Values: Reconfiguring Kinship Studies*, edited by S. Franklin and S. McKinnon. Durham: Duke University Press.

Carsten, J., and S. Hugh-Jones. 1995. Introduction. In *About the House: Levi-Strauss and Beyond*, edited by J. Carsten and S. Hugh-Jones. Cambridge: CUP.

Carsten, Janet. 1991. Children In Between: Fostering and the process of kinship on Pulau Langkawi, Malaysia. *Man* 26:425-443.

———. 1995. The substance of kinship and the heat of the hearth: feeding, personhood, and relatedness among Malays in Pulau Langkawi. *American Ethnologist* 22 (2):223-241.

———. 2000. Introduction: cultures of relatedness. In *Cultures of relatedness: new approaches to the study of kinship*, edited by J. Carsten. Cambridge: CUP.

Cavalli-Sforza, L. L., and M.W. Feldman. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton, NJ: Princeton University Press.

Chagnon, Napoleon A. 1979. Mate Competition, Favouring Close Kin, and Village Fissioning Among the Yanomamo Indians. In *Evolutionary biology and human social behaviour: An anthropological perspective*, edited by N. A. Chagnon and W. Irons. North Scituate, Mass: Duxbury Press.

Chagnon, N. A., & Bugos, P. 1979. Kin selection and conflict: An analysis of a Yanomamö ax fight. In *Evolutionary biology and human social behaviour: An* *anthropological perspective*, edited by N. A. Chagnon and W. Irons. North Scituate, Mass: Duxbury Press.

Chapais, B. 2001. Primate nepotism: What is the explanatory value of kin selection? *International Journal of Primatology* 22 (2):203-229.

Charnov, E. L. 1993. *Life History Invariants: Some explorations of symmetry in evolutionary ecology*. Oxford: OUP.

Clarke, A. L., B. E. Saether, and E. Roskaft. 1997. Sex biases in avian dispersal: A reappraisal. *Oikos* 79 (3):429-438.

Clutton-Brock, T. H. 1989. Female Transfer and Inbreeding Avoidance in Social Mammals. *Nature* 337 (6202):70-72.

———. 1989. Mammalian Mating Systems. *Proceedings of the Royal Society of London Series B-Biological Sciences* 236 (1285):339-372.

Clutton-Brock, T.H., and P.H. Harvey. 1978. Mammals, resources and reproductive strategies. *Nature* 273 (5659):191-5.

Clutton-Brock, T. 2002. Behavioral ecology - Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* 296 (5565):69-72.

Cockburn, A., M. P. Scott, and D. J. Scotts. 1985. Inbreeding Avoidance and Male-Biased Natal Dispersal in Antechinus Spp (Marsupialia, Dasyuridae). *Animal Behaviour* 33 (AUG):908-915.

Cohen, Yehudi A. 1961[1955]. Food and its Vicissitudes: A cross-cultural study of sharing and non-sharing. In *Social Structure and Personality: A Casebook*, edited by Y. A. Cohen. New York: Holt, Rinehart and Winston.

Collier, Jane Fishburne, and Sylvia Junko Yanagisako. 1987. *Gender and kinship : essays toward a unified analysis*. Stanford, CA: Stanford University Press.

Crawley, Ernest. 1902. *The Mystic Rose: A Study of Primitive Marriage and of Primitive Thought in Its Bearing on Marriage*. London: Macmillan.

Crnokrak, P., and D. A. Roff. 1999. Inbreeding depression in the wild. *Heredity* 83:260-270.

Crook, J. H. 1964. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). *Behaviour Suppl* 10:1-178.

———. 1970. *Social Behaviour in Birds and Mammals*. New York: Academic Press.

Cucchiari, Salvatore. 1981. The Gender revolution and the transition from a bisexual horde to patrilocal band: The origins of gender hierarchy. In *Sexual Meanings: the cultural construction of gender and sexuality*, edited by S. Ortner and H. Whitehead. Cambridge: CUP.

Daly, E. M., and Margo Wilson. 1996. Evolutionary psychology and marital conflict: the relevance of stepchildren. In *Sex, power, conflict: feminist and evolutionary perspectives*, edited by D. Buss and N. Malamuth. New York: OUP.

Daly, M., C. Salmon, and M.I. Wilson. 1997. Kinship: the conceptual hole in psychological studies of social cognition and close relationships. In *Evolutionary social psychology*, edited by J. A. Simpson and D. Kenrick. Mahwah NJ: Erlbaum.

Daly, Martin, and Margo I. Wilson. 1999. An evolutionary psychological perspective on homicide. In *Homicide Studies: A Sourcebook of Social Research*, edited by D. Smith and M. Zahn.

D'Andrade, Roy G. 1995. Moral Models in Anthropology. *Current Anthropology* 36 (3):399-408.

Darwin, Charles. 1859. *On the origin of species by means of natural selection, or The preservation of favoured races in the struggle for life*. London: John Murray.

Davis, Diana. 1984. Adult Male-Infant Interactions in the Chimpanzee. In *Primate Paternalism*, edited by M. Taub. New York: Van Nostrand Reinhold.

Dawkins, Richard. 1976. *The Selfish Gene*. New ed. London: OUP

———. 1979. 12 Misunderstandings of kin selection. *Z. Tierpsychology* 51:184-200.

———. 1982. *The Extended Phenotype: The Gene as the Unit of Selection*. San Francisco: Freeman.

———. 1989. *The Selfish Gene, 2nd Edition*. New ed. London.OUP.

———. 1999. *The Extended Phenotype: The long reach of the gene*. Oxford: Oxford Paperbacks.

de Charlevoix, P. 1744. *Journal of a Voyage to North America*. London: Dodsley.

de Matos Viegas, S. 2003. Eating with your favourite mother: Time and sociality in a Brazilian Amerindian community. *Journal of the Royal Anthropological Institute* 9 (1):21-37.

Disotell, Todd R. 2000. Molecular Anthropology and Race. *Annals of the New York Academy of Sciences* 925:9-24.

Dolhinow, Phyllis, ed. 1972. *Primate Patterns*. New York: Holt Rinehart and Winston.

Doncaster, C. P., J. Clobert, B. Doligez, L. Gustafsson, and E. Danchin. 1997. Balanced dispersal between spatially varying local populations: An alternative to the source-sink model. *American Naturalist* 150 (4):425-445.

Easterbrooks, M. Ann, and Robert N. Emde. 1988. Marital and parent-child relationships: the role of affect in the family system. In *Relationships within Families: Mutual Influences*, edited by R. A. Hinde and J. Stevenson-Hinde. Oxford: Clarendon Press.

Eibl-Eibesfeldt. 1989. *Human Ethology*. New York: Aldine de Gruyter.

Ember, Carol R. 1975. Residential Variation Among Hunter-Gatherers. *Behavior Science Research* 10:199-227.

Ember, M., and C.R. Ember. 1971. The Conditions Favouring Matrilocal Versus Patrilocal Residence. *American Anthropologist* 73:571-594.

Emlen, S., and L. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.

Endicott, Karen. 1992. Fathering in an egalitarian society. In *Father-child relations: Cultural and biosocial contexts*, edited by B. S. Hewlett. New York: Aldine de Gruyter.

Engels, Friedrich. 1884. *Der Ursprung der Familie, des Privateigenthums und des Staats*. Hottingen Zurich: Verlag der Shweizerischen Volkbuchbandlung.

Erhart, E. M., A. M. Coelho, and C. A. Bramblett. 1997. Kin recognition by paternal half-siblings in captive Papio cynocephalus. *American Journal of Primatology* 43 (2):147-157.

Evans-Pritchard, E.E. 1940. *The Nuer: A Description of the Modes of Livelihood and Political Institutions of a Nilotic People*. Oxford: Clarendon.

———. 1951. *Kinship and Marriage among the Nuer*. Oxford: Clarendon.

Fedigan, Linda M., and Shirley C. Strum. 1999. A Brief History of Primate Studies. In *The Nonhuman Primates*, edited by P. Dolhinow and A. Fuentes. Mountain: Mayfield.

Feinberg, Richard. 2001. Introduction: Schneider's Cultural Analysis of Kinship and Its Implications for Anthropological Relativism. In *The cultural analysis of kinship : the legacy of David M. Schneider*, edited by R. Feinberg and M. Ottenheimer. Urbana: University of Illinois Press.

Feistner, A.T.C., and W.C. McGrew. 1989. Food sharing in non-human Primates: A critical review. In *Perspectives in Primate Biology*, edited by P. K. Seth and S. Seth. New Delhi: Today and Tomorrow's Press.

Firth, R.W. 1934. The sociological study of native diet. *Africa* 7:401-414.

Firth, Raymond William. 1956. *Two studies of kinship in London*. [London]: University of London Athlone Press.

Fisher, Ronald A. 1958. *The genetical theory of natural selection*. 2nd ed. New York: Dover.

Flinn, M. 1985. commentary on Hartung "Matrilineal Inheritance: New theory and Analysis". *The Behavioural and Brain Sciences* 8 (4):673-674.

Flinn, Mark. 1981. Uterine vs. Agnatic Kinship Variability and Associated Cousin Marriage Preferences: An Evolutionary Biological Analysis. In *Natural Selection and Social Behavior: Recent Research and New Theory*, edited by R. D. Alexander and D. W. Tinkle. New York: Chiron Press.

Fortes, M. 1936. Food in the domestic economy of the Tallensi. *Africa* 9:1-23.

———. 1958. Introduction. In *The developmental cycle in domestic groups*, edited by J. Goody. Cambridge Eng.: Published for the Dept. of Archaeology and Anthropology at the University Press.

Fortes, Meyer. 1969. *Kinship and the social order: the legacy of Lewis Henry Morgan*. Chicago: Aldine.

Fox, R. 1985. Paternity Certainty or Paternity Irrelevance? *The Behavioural and Brain Sciences* 8 (4):674-675.

Fox, Robin. 1993. *Reproduction and succession: Studies in anthropology, law, and society*. New Brunswick: Transaction.

———. 1996. Sociobiology. In *The Social Science Encyclopedia*, edited by A. Kuper and J. Kuper. London: Routledge.

Frank, Steven A. 1995. George Price's contributions to evolutionary genetics. *Journal of Theoretical Biology* 175:373-377.

———. 1997. Multivariate Analysis of Correlated Selection and Kin Selection, with an ESS Maximization Method. *Journal of Theoretical Biology* 189:307-316.

Freedman, M. 1979. *The study of the Chinese society: essays by Maurice Freedman Selected and Introduced by G. W. Skinner*. Stanford: Stanford University Press.

Fruth, Barbara, Gottfried Hohmann, and William McGrew, C. 1999. The Pan Species. In *The Nonhuman Primates*, edited by P. Dolhinow and A. Fuentes. Mountain View: Mayfield.

Fuentes, A. 2000. Hylobatid communities: Changing views on pair bonding and social organisation in hominoids. *Yearbook of Physical Anthropology* 43:33-60.

Fuentes, Agustin. 1999. Variable Social Organisation: What can looking at primates tell us about the evolution of plasticity in primate societies? In *The Nonhuman Primates*, edited by P. Dolhinow and A. Fuentes. Mountain View: Mayfield.

Gabor, C. R. 1996. Differential kin discrimination by red-spotted newts (Notophthalmus viridescens) and smooth newts (Triturus vulgaris). *Ethology* 102 (8):649-659.

Galvin, Kathey-Lee. 2001. Schneider Revisited: Sharing and Ratification in the Construction of Kinship. In *New directions in anthropological kinship*, edited by L. Stone. Lanham: Rowman & Littlefield Publishers.

Gamboa, G. J., H. K. Reeve, and W. G. Holmes. 1991. Conceptual Issues and Methodology in Kin-Recognition Research - a Critical Discussion. *Ethology* 88 (2):109-127.

Gaulin, Steven J.C., and Alice Schlegel. 1980. Paternal Confidence and Paternal Investment: A Cross Cultural Test of a Sociobiological Hypothesis. *Ethology and Sociobiology* 1:301-309.

Geertz, C. 1973. Thick description: Toward an interpretive theory of culture. In *The interpretation of cultures*, edited by C. Geertz. New York: Basic Books.

Geiger, Brenda. 1996. *Fathers as Primary Caregivers*. London: Greenwood Press.

Goldsmith, Michele. 1999. Gorilla Socioecology. In *The Nonhuman Primates*, edited by P. Dolhinow and A. Fuentes. Mountain: Mayfield.

Gonzalez, S. G., and P. J. Goddard. 1998. The provision of supplementary colostrum to newborn lambs: effects on post-natal lamb and ewe behaviour. *Applied Animal Behaviour Science* 61 (1):41-50.

Goodenough, Ward H. 2001. Conclusions: Muddles in Schneider's Model. In *The cultural analysis of kinship : the legacy of David M. Schneider*, edited by R. Feinberg and M. Ottenheimer. Urbana: University of Illinois Press.

Goody, Jack. 1958. *The developmental cycle in domestic groups*, *Cambridge papers in social anthropology, no. 1*. Cambridge Eng.: Published for the Dept. of Archaeology and Anthropology at the University Press.

———. 1969. Adoption in Cross-Cultural Perspective. *Comparative Studies in Society and History* 11 (1):55-78.

Gough, Kathleen. 1975 [1971]. The Origin of the Family. In *Toward an anthropology of women*, edited by R. R. Reiter. New York: Monthly Review Press.

Gould, S.J., and R.C. Lewontin. 1979. The spandrels of San Marco and the Panglosian paradigm: A critique of the Adaptationist Programme. *Proceedings Of The Royal Society Of London. Series B: Biological Sciences* 205:581-598.

Gould, S.J., and E.S. Vrba. 1982. Exaptation-a missing term in the science of form. *Paleobiology* 8 (1):4-15.

Gouzoules, Sarah, and Harold Gouzoules. 1987. Kinship. In *Primate Societies*, edited by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker. Chicago: The University of Chicago Press.

Gow, Peter. 1991. *Of mixed blood: kinship and history in Peruvian Amazonia.* Oxford: Clarendon Press.

Grafen, A. 1990. Do animals really recognize kin? *Animal Behaviour* 39:42-54.

Grafen, A. 1991. Development, the Conveniently Forgotten Variable in True Kin Recognition - Reply. *Animal Behaviour* 41:1091-1092.

———. 1991. Kin Recognition in Vertebrates - What Do We Really Know About Adaptive Value - Reply. *Animal Behaviour* 41:1085-1087.

———. 1991. Kin Vision - Reply. *Animal Behaviour* 41:1095-1096.

Grafen, Alan. 1984. Natural Selection, Kin Selection and Group Selection. In *Behavioural Ecology: An evolutionary Approach*, edited by J. R. Krebs and N. B. Davies. Oxford: Blackwell Scientific Publications.

———. 1985. A geometric view of relatedness. In *Oxford Surveys in Evolutionary Biology 2*, edited by R. Dawkins and M. Ridley. Oxford: OUP.

Green, W. C. H. 1993. Social Effects of Maternal Age and Experience in Bison - Preweaning and Post-Weaning Contact Maintenance with Daughters. *Ethology* 93 (2):146-160.

Greene, Penelope J. 1978. Promiscuity, Paternity and Culture. *American Ethnologist* 5:151-159.

Gubernick, David J. 1981. Parent and Infant Attachment in Mammals. In *Parental Care in Mammals*, edited by D. J. Gubernick and Klopfer. New York: Plenum.

Guemple, Lee. 1979. Inuit Adoption. *Canadian Ethnology Service Paper No. 47; National Museum of Man Mercury Series.*

Guerra, R.F., E. Takese, and C.V. Santos. 1998. Cross-Fostering Between Two Species of Marmosets (Callithrix jacchus and Callithrix penicillata). *Revista Brasiliera Biologia* 58 (4):665-669.

Gutmann, B. 1926. *Das Recht der Dschagga*. Munich.

Haig, D. 1997. Parental antagonism, relatedness asymmetries, and genomic imprinting. *Proceedings Of The Royal Society Of London. Series B: Biological Sciences* 264 (1388):1657-62.

Haldane, J. B. S. 1932. *The Causes of Evolution*. London: Longmans.

Haldane, J.B.S., and S.D. Jayakar. 1962. An Enumeration of Some Human Relationships. *Journal of Genetics* 58:81-107.

Halpin, Z.T. 1991. Kin recognition cues of vertebrates. In *Kin Recognition*, edited by P. G. Hepper. Cambridge: CUP.

Hamilton, W. D. 1971. Selection of selfish and altruistic behaviour in some extreme models. In *Man and Beast: Comparative Social Behavior*, edited by J. F. Eisenberg and W. S. Dillon. Washington DC: Smithsonian Press.

———. 1987. Discriminating nepotism: expectable, common and overlooked. In *Kin recognition in animals*, edited by D. J. C. Fletcher and C. D. Michener. New York: Wiley.

———. 1996. *Narrow Roads of Gene Land*. Vol. 1. Oxford: W. H. Freeman.

Hamilton, William D. 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* 228:1218-1220.

———. 1972. Altruism and Related Phenomena, Mainly in Social Insects. *Annual Review of Ecology and Systematics* 3:193-232.

———. 1975. Innate social aptitudes of man: an approach from evolutionary genetics. In *ASA Studies 4: Biosocial Anthropology*, edited by R. Fox. London: Malaby Press.

Hamilton, William D. 1963. The Evolution of Altruistic Behaviour. *American Naturalist* 97:354-356.

———. 1964. The Genetical Evolution of Social Behaviour. *Journal of Theoretical Biology* 7:1-52.

Hanggi, E. B., and R. J. Schusterman. 1990. Kin Recognition in Captive California Sea Lions (Zalophus- Californianus). *Journal of Comparative Psychology* 104 (4):368-372.

Hare, J. F. 1992. Colony Member Discrimination by Juvenile Columbian Ground-Squirrels (Spermophilus-Columbianus). *Ethology* 92 (4):301-315.

Hare, J. F., and J. O. Murie. 1996. Ground squirrel sociality and the quest for the "holy grail": Does kinship influence behavioral discrimination by juvenile Columbian ground squirrels. *Behavioral Ecology* 7 (1):76-81.

Harlow, H.F. 1986. *From Learning to Love*. New York: Praeger.

Hartland, E.S. 1909. *Primitive Paternity*. 2 vols. London: David Nutt.

Hartung, John. 1976. On Natural Selection and the Inheritance of Wealth. *Current Anthropology* 17 (4):607-622.

———. 1985. Matrilineal inheritance: New theory and analysis. *The Behavioural and Brain Sciences* 8 (4):661-688.

———. 1997. If I Had To Do It Over. In *Human Behaviour*, edited by L. Betzig. Oxford: OUP.

Hartwig, W.C. 1999. Primate Evolution. In *The Nonhuman Primates*, edited by P. Dolhinow and A. Fuentes. Mountain View: Mayfield.

Hauber, M. E., and P. W. Sherman. 2001. Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends in Neurosciences* 24 (10):609-616.

Hawkes, K., J. F. O'Connell, and N. G. B. Jones. 2001. Hunting and nuclear families - Some lessons from the Hadza about men's work. *Current Anthropology* 42 (5):681-709.

Hawkes, K., J. F. O'Connell, N. G. B. Jones, H. Alvarez, and E. L. Charnov. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences of the United States of America* 95 (3):1336-1339.

Heino, M., and I. Hanski. 2001. Evolution of migration rate in a spatially realistic metapopulation model. *American Naturalist* 157 (5):495-511.

Hepper, Peter G. 1991. Recognizing kin: ontogeny and classification. In *Kin Recognition*, edited by P. G. Hepper. Cambridge: CUP.

Hernandez, H., N. Serafin, A. M. Terrazas, P. G. Marnet, G. Kann, J. A. Delgadillo, and P. Poindron. 2002. Maternal olfaction differentially modulates oxytocin and prolactin release during suckling in goats. *Hormones and Behavior* 42 (2):232-244.

Heth, G., J. Todrank, and R. E. Johnston. 1998. Kin recognition in golden hamsters: evidence for phenotype matching. *Animal Behaviour* 56:409-417.

Hewlett, B. 2001. Neoevolutionary Approaches to Human Kinship. In *New Directions in Anthropological Kinship*, edited by L. Stone. Oxford: Rowman and Littlefield.

Hirschfeld, L.A. 1994. Is the Acquisition of Social Categories based on Domain Specific Competence or on Knowledge Transfer? In *Mapping the Mind: Domain Specificity in Cognition and Culture*, edited by L. A. Hirschfeld and S. A. Gellman. Cambridge: CUP.

Hohmann, Gottfried, and Barbara Fruth. 1996. Food sharing and status in unprovisioned bonobos. In *Food and the Status Quest an interdisciplinary perspective*, edited by P. Weissner and Schiefenhövel. Providence: Berghahn Books.

Holmes, W. G. 1995. The Ontogeny of Littermate Preferences in Juvenile Golden-Mantled Ground-Squirrels - Effects of Rearing and Relatedness. *Animal Behaviour* 50:309-322.

Holmes, W. G., and P. W. Sherman. 1982. The ontogeny of kin recognition in two species of ground squirrels. *American Zoologist* 22:491-517.

Holmes, W. G., and P. W. Sherman. 1983. Kin recognition in animals. *American Scientist* 71:46-55.

Holmes, W. G. 1990. Parent–offspring recognition in mammals: a proximate and ultimate perspective. In *Mammalian parenting : biochemical, neurobiological, and behavioral determinants*, edited by N. A. Krasnegor and R. S. Bridges. Oxford: OUP

Holy, Ladislav. 1996. *Anthropological perspectives on kinship*, *Anthropology, culture and society*. London ; Chicago: Pluto Press.

Houpt, K. A. 2002. Formation and dissolution of the mare-foal bond. *Applied Animal Behaviour Science* 78 (2-4):319-328.

Hrdy, S. B. 1977. *The Langurs of Abu. Female and Male Strategies of Reproduction*. Cambridge, Mass: Harvard University Press.

Hrdy, S. B. 1999. *Mother Nature; a history of mothers, infants and natural selection*. New York: Pantheon Books.

Hrdy, S. B. 2000. The optimal number of fathers - Evolution, demography, and history in the shaping of female mate preferences. In *Evolutionary Perspectives On Human Reproductive Behavior*.

Hull, C. L. 1943. *Principles of behavior*. New York: Appleton-Century-Crofts.

Huxley, Thomas Henry. 1893. *Evolution and Ethics*. London: Macmillan.

Ingold, Tim. 2000. *The perception of the environment: essays on livelihood, dwelling and skill*. London: Routledge.

Irons, William. 1979. Natural Selection, Adaptation and Human Social Behaviour. In *Evolutionary biology and human social behaviour: An Anthropological Perspective*, edited by N. A. Chagnon and W. Irons.

Isbell, L. and D. VanVuren. 1996. Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* 133:1-36.

Jackel, M., and F. Trillmich. 2003. Olfactory individual recognition of mothers by young guinea-pigs (Cavia porcellus). *Ethology* 109 (3):197-208.

Janowski, Monica. 1995. The hearth-group, the conjugal couple and the symbolism of the rice meal among the Kelabit of Sarawak. In *About the House: Levi-Strauss and Beyond*, edited by J. Carsten and S. Hugh-Jones. Cambridge: CUP.

Janzen, M. I. D., P. J. A. Timmermans, J. P. Kruijt, and J. M. H. Vossen. 1999. Do young guinea pigs (Cavia porcellus) develop an attachment to inanimate objects? *Behavioural Processes* 47 (1):45-52.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.

Jay, P. 1965. The common Langur of north India. In *Primate Behavior: field studies of monkeys and apes*, edited by I. DeVore. New York: Holt, Rinehart, Winston.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of Dispersal - Theoretical-Models and Empirical Tests Using Birds and Mammals. *Annual Review of Ecology and Systematics* 21:449-480.

Johnstone, Rufus A. 1997. Recognition and the Evolution of Distinctive Signatures: When does it pay to reveal identity? *Proceedings of the Royal Society of London* 264 (1387):1547-1553.

Johst, K., and R. Brandl. 1997. Evolution of dispersal: The importance of the temporal order of reproduction and dispersal. *Proceedings of the Royal Society of London Series B-Biological Sciences* 264 (1378):23-30.

Kappeler, P.M., M.E. Pereira, and C.P. van Schaik. 2003. Primate life histories and socioecology. In *Primate Life History and Socioecology*, edited by P. M. Kappeler and M. E. Pereira. Chicago: University of Chicago Press.

Kapsalis, E., and C.M. Berman. 1996. Models of affiliative relationships among free-ranging rhesus monkeys (Macaca mulatta). *Behaviour* 133:1209-1234.

Keller, L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17 (5):230-241.

Kitcher, P.S. 1985. *Vaulting Ambition: Sociobiology and the Quest for Human Nature*. Cambridge, Mass: MIT press.

Kokko, H., R. A. Johnstone, and T.H. Clutton-Brock. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268 (1427):187-196.

Korchmaros, J.D., and D.A. Kenny. 2001. Emotional closeness as a mediator of the effect of genetic relatedness on altruism. *Psychological Science* 12:262-265.

Kroeber, A.L. 1938. Basic and Secondary patterns of social structure. *Journal of the Royal Anthropological Institute* 68:299-309.

Kuper, Adam. 1982. Lineage theory: a critical retrospective. *Annual Review of Anthropology* 11:71-95.

Kurland, J. A. 1977. Kin selection in the Japanese monkey. In *Contributions to primatology*. Basel: Karger.

Kurland, J.A. 1979. Paternity, Mother's Brother, and Human Sociality. In *Evolutionary biology and human social behaviour*, edited by N. A. Chagnon and W. Irons. North Scituate, Mass.: Duxbury Press.

Kurland, J.R. 1985. commentary on Hartung "Matrilineal Inheritance: New theory and Analysis". *The Behavioural and Brain Sciences* 8 (4):675-676.

Lacy, R. C. 1997. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* 78 (2):320-335.

Lacy, R.C., and P. W. Sherman. 1983. Kin recognition by phenotype matching. *American Naturalist* 121:489-512.

Lamb, M. E., Thompson, R. A., Gardner, W., & Charnov, E. L. (1985). *Infant-mother attachment: The origins and developmental significance of individual differences in Strange Situation behavior.* Hillsdale, N.J: LEA.

Lamb, Michael E. 1997. The Development of the Father-Infant Relationship. In *The Role of the Father in Child Development*, edited by M. E. Lamb. New York: Wiley.

Lambert, Helen. 2000. Sentiment and Substance in North Indian forms of Relatedness. In *Cultures of Relatedness: New approaches to the study of Kinship*, edited by J. Carsten. Cambridge: CUP.

Lambin, X. 1994. Natal Philopatry, Competition for Resources, and Inbreeding Avoidance in Townsends Voles (Microtus-Townsendii). *Ecology* 75 (1):224-235.

Lancaster. 1985. commentary on Hartung "Matrilineal Inheritance: New theory and Analysis". *The Behavioural and Brain Sciences* 8 (4):676-677.

Langness, L.L. 1964. Some problems in the conceptualization of Highlands social structures. *American Anthropologist* 66 (3):162-182.

Lawson, J. W., and D. Renouf. 1987. Bonding and Weaning in Harbor Seals, Phoca-Vitulina. *Journal of Mammalogy* 68 (2):445-449.

Lee, Richard B., and Irven DeVore, eds. 1968. *Man the Hunter*. Chicago: Aldine.

Lowe, E. D. 2002. A widow, a child, and two lineages: Exploring kinship and attachment in Chuuk. *American Anthropologist* 104 (1):123-137.

Lowie, Robert H. 1947 [1920]. *Primitive Society*. New York: Boni & Liveright.

Lumsden, Charles J., and Edward O. Wilson. 1983. *Promethean Fire: Reflections on the Origin of Mind*. London: Harvard University Press.

Lyons, Sherrie L. 1999. *Thomas Henry Huxley: the evolution of a scientist.* Amherst, New York: Prometheus Books.

MacArthur, R.H., and E.O. Wilson, eds. 1967. *The theory of Island Biogeography*, *Monographs in Population Biology 1*. Princeton: Princeton University Press.

MacDonald, David W., ed. 1995. *The Encyclopedia of Mammals*. London: Checkmark.

Macgregor, G. 1946. *Warriors without weapons*. Chicago: University of Chicago Press.

Maine, Henry S. 1861. *Ancient law, its connection with the early history of society and its relation to modern ideas*. London: Murray.

Malinowski, B. 1930. Parenthood - the basis of social structure. In *The New Generation*, edited by V. Calverton and S. D. Schmalhausen. New York: Macaulay.

———. 1930A. Kinship. *Man* 30 (2):19-29.

———. 1930B. Parenthood - the basis of social structure. In *The New Generation*, edited by V. Calverton and S. D. Schmalhausen. New York: Macaulay.

Malinowski, Bronislaw. 1913. *The family among the Australian Aborigines: a Sociological Study*. London: University of London Press.

Marlowe, F. 1999. Male care and mating effort among Hadza foragers. *Behavioral Ecology and Sociobiology* 46:57-64.

———. 2001. Male contribution to diet and female reproductive success among foragers. *Current Anthropology* 42 (5):755-760.

Marsden, Stella. 2000. *Chimpanzees: Return to the Forest*. Nature Conservation Films

Marshall, Mac. 1977. The Nature of Nurture. *American Ethnologist* 4 (4):643-662.

Mathias, A., E. Kisdi, and I. Olivieri. 2001. Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* 55 (2):246-259.

Mauss, Marcel. 1967 [1925]. *The Gift*. Translated by I. Cunnison. New York: Norton.

Maybury-Lewis, D. 1965. Durkheim on Relationship Systems. *Journal of Scientific Study of Religion* 4:253-206.

Maynard Smith, J. 1976. Group Selection. *Quarterly Review Of Biology* 51:277-283.

Maynard Smith, John. 1964. Group Selection and Kin Selection. *Nature* 201 (14 March):1145-1147.

McGrew, W.C. 1996. Dominance status, food sharing and reproductive success in chimpanzees. In *Food and the Status Quest an interdisciplinary perspective*, edited by P. Weissner and Schiefenhövel. Providence: Berghahn Books.

McKenna, James J. 1987. Parental Supplements and Surrogates Among Primates: Cross-Species and Cross-Cultural Comparisons. In *Parenting Across the Life Span: Biosocial Dimensions*, edited by J. B. Lancaster, J. Altmann, A. Rossi and L. Sherrod. New York: Aldine DeGruyter.

McKinley, Robert. 2001. The Philosophy of Kinship: A Reply to Schneider's Critique of the Study of Kinship. In *The cultural analysis of kinship : the legacy of David M. Schneider*, edited by R. Feinberg and M. Ottenheimer. Urbana: University of Illinois Press.

McPeek, M. A., and R. D. Holt. 1992. The Evolution of Dispersal in Spatially and Temporally Varying Environments. *American Naturalist* 140 (6):1010-1027.

Mead, M. 1928. *Coming of Age in Samoa*. New York: William Morrow.

Mead, Margaret. 1935. *Sex and Temperament in Three Primitive Societies*. New York: William Morrow.

Meigs, Anna. 1989. The cultural construction of reproduction and its relationship to gender (New Guinea highlands). In *Culture, Kin and Cognition in Oceania: Essays in Honor of Ward H. Goodenough*, edited by M. Marshall and J. L. Caughey. Washington, D.C.: American Anthropological Association.

———. 1997. Food as a Cultural Construction. In *Food and Culture: A reader*, edited by C. Counihan and P. Van Esterik. London: Routledge.

Mekosh Rosenbaum, V., W. J. Carr, J. L. Goodwin, P. L. Thomas, A. Dver, and C. J. Wysocki. 1994. Age-Dependent Responses to Chemosensory Cues Mediating Kin Recognition in Dogs (Canis-Familiaris). *Physiology & Behavior* 55 (3):495-499.

Michod, R.E., and W. D. Hamilton. 1980. Coefficients of Relatedness in Sociobiology. *Nature* 288:694-697.

Modern Universal History. 1759. edited by Richardson.

Montague, Susan P. 2001. The Trobriand Kinship Classification and Schneider's Cultural Relativism. In *The cultural analysis of kinship : the legacy of David M. Schneider*, edited by R. Feinberg and M. Ottenheimer. Urbana: University of Illinois Press.

Moore, Henrietta L. 1999. *Anthropological theory today*. Cambridge England ; Malden, MA: Polity Press.

Moore, J. 1992. Dispersal, Nepotism, and Primate Social-Behavior. *International Journal of Primatology* 13 (4):361-378.

Morgan, L. H. 1877. *Ancient Society*. London: Macmillan.

Morgan, Lewis Henry. 1870. *Systems of consanguinity and affinity of the human family*. Vol. 17, *Smithsonian Contributions to Knowledge*. Washington, DC: Smithsonian Institution.

Motro, U. 1991. Avoiding Inbreeding and Sibling Competition - the Evolution of Sexual Dimorphism for Dispersal. *American Naturalist* 137 (1):108-115.

Murdock, George Peter. 1949. *Social Structure*. New York: Macmillan.

———. 1967. *Ethnographic Atlas*. Pittsburgh: University of Pittsburgh Press.

Needham, Rodney. 1971. Remarks on the Analysis of Kinship and Marriage. In *Rethinking kinship and marriage*, edited by R. Needham. London: Tavistock Publications.

———. 1971. *Rethinking kinship and marriage*, *A.S.A. monograph ; 11*. London: Tavistock Publications.

Nicolson, N. 1982. Weaning and the development of independence in olive baboons. Ph.D. Thesis, Harvard University, Cambridge, MA.

Nicolson, Nancy A. 1987. Infants, Mothers and Other Females. In *Primate Societies*, edited by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker. Chicago: The University of Chicago Press.

Nishida, T., and L. Turner. 1996. Food transfer between mother and infant chimpanzees of the Mahale Mountains National Park, Tanzania. *International Journal of Primatology* 17:947-968.

Nowak, M. A., Tarnita, C. E., and Wilson, E. O. 2010. The evolution of eusociality. *Nature*, 466(7310):1057-1062.

Nuttall, Mark. 2000. Choosing Kin: Sharing and subsistence in a Greenlandic hunting community. In *Dividends of kinship : meanings and uses of social relatedness*, edited by P. P. Schweitzer. New York: Routledge.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 103 (589-603).

Osawa, N. 1992. Sibling Cannibalism in the Ladybird Beetle Harmonia-Axyridis - Fitness Consequences for Mother and Offspring. *Researches on Population Ecology* 34 (1):45-55.

Overing, Joanna, and Alan Passes. 2000. *The anthropology of love and anger : the aesthetics of conviviality in Native Amazonia*. New York: Routledge.

Pader, E. J. 1993. Spatiality and Social-Change - Domestic Space Use in Mexico and the United-States. *American Ethnologist* 20 (1):114-137.

Pagel, M. 1997. Desperately concealing father: A theory of parent-infant resemblance. *Animal Behaviour* 53:973-981.

Palombit, R. A. 1999. Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology* 7 (4):117-129.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67 (4):518-536.

Parish, Steven M. 1994. *Moral Knowing in a Hindu Sacred City: An Exploration of Mind, Emotion, and Self.* New York: Columbia University Press.

Parkin, Robert. 1997. *Kinship: An Introduction to Basic Concepts*. Oxford: Blackwell.

Pasternak, Burton, Carol R. Ember, and Melvin Ember. 1997. *Sex, gender, and kinship : a cross-cultural perspective*. Upper Saddle River, N.J.: Prentice Hall.

Paul, A., J. Kuester, A. Timme, and J. Arnemann. 1993. The Association between Rank, Mating Effort, and Reproductive Success in Male Barbary Macaques (Macaca-Sylvanus). *Primates* 34 (4):491-502.

Paul, Andreas, Signe Preuschoft, and Carel P. van Schaik. 2000. The other side of the coin: infanticide and the evolution of affiliative male-infant interactions in Old World primates. In *Infanticide by males and its implications*, edited by C. van Schaik and C. H. Jansen. Cambridge: CUP.

Perrin, N., and V. Mazalov. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist* 155 (1):116-127.

Phillpotts, Bertha. 1913. *Kindred and Clan*. Cambridge: CUP.

Pinker, Steve. 1999. The Blank Slate, the Noble Savage, and the Ghost in the Machine, The Tanner Lectures on Human Values, Yale University, Yale.

Pitt-Rivers, J. 1973. The Kith and the Kin. In *The Character of Kinship*, edited by J. Goody. Cambridge: Cambridge University Success.

Porter, R. H. 1988. The Ontogeny of Sibling Recognition in Rodents - Superfamily Muroidea. *Behavior Genetics* 18 (4):483-494.

Porter, R. H., F. Levy, P. Poindron, M. Litterio, B. Schaal, and C. Beyer. 1991. Individual Olfactory Signatures as Major Determinants of Early Maternal Discrimination in Sheep. *Developmental Psychobiology* 24 (3):151-158.

Preston, S. D., and F. B. M. de Waal. 2002. Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences* 25 (1):1-+.

Price, George C. 1970. Selection and Covariance. *Nature* 227 (01 August):520-521.

Pusey, A., and M. Wolf. 1996. Inbreeding avoidance in animals. *Trends in Ecology & Evolution* 11 (5):201-206.

Pusey, Anne E., and Craig Packer. 1987. Dispersal and Philopatry. In *Primate Societies*, edited by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker. Chicago: The University of Chicago Press.

Queller, D.C. 1992. A general model for kin selection. *Evolution* 46:376-380.

Radcliffe-Brown, A. R. 1922. *The Andaman Islanders*. Cambridge: CUP.

———. 1950. Introduction. In *African systems of kinship and marriage*, edited by A. R. Radcliffe-Brown and C. D. Forde. London: OUP.

Reichard, U., and V. Sommer. 1997. Group encounters in wild gibbons (Hylobates lar): Agonism, affiliation, and the concept of infanticide. *Behaviour* 134:1135-1174.

Ribble, D. O. 1992. Dispersal in a Monogamous Rodent, Peromyscus-Californicus. *Ecology* 73 (3):859-866.

Richards, A.I. 1932. *Hunger and Work in a Savage Tribe: A functional study of Nutrition among the Southern Bantu*. London: G. Routledge and sons.

Richardson, P.J., and R. Boyd. 2001. Culture is Part of Human Biology. In *Science Studies: Probing the Dynamics of Scientific Knowledge*, edited by S. Maasen and M. Winterhager: Verlag.

Ridley, Mark, ed. 1997. *Evolution*, *Oxford Readers*. Oxford: OUP.

Rival, L. 1998. Androgynous parents and guest children: The Huaorani couvade. *Journal of the Royal Anthropological Institute* 4 (4):619-642.

Roberson Smith, William. 1889. *Lectures on the Religion of the Semites*. London: Black.

Romeyer, A. 1993. Ontogeny and Selectivity of the Mother-Young Bond in Sheep and Goats. *Revue D Ecologie-La Terre Et La Vie* 48 (2):143-153.

Romeyer, A., and P. Poindron. 1992. Early Maternal Discrimination of Alien Kids by Post-parturient Goats. *Behavioural Processes* 26 (2-3):103-111.

Rothbard, Julie C., and Phillip R. Shaver. 1994. Continuity of Attachment across the Life Span. In *Attachment in Adults: Clinical and Developmental Perspectives*, edited by M. B. Sperling and W. H. Berman. New York: The Guilford Press.

Rubenstein, Dan, and Richard Wrangham. 1986. Socioecology: Origins and Trends. In *Ecological Aspects of Social Evolution*, edited by D. Rubenstein and R. Wrangham. Princeton, NJ: Princeton University Press.

Ruiz-Miranda, C. R., S. A. Wells, R. Golden, and J. Seidensticker. 1998. Vocalizations and other behavioral responses of male cheetahs (Acinonyx jubatus) during experimental separation and reunion trials. *Zoo Biology* 17 (1):1-16.

Sahlins, M. 1976. *The use and abuse of Biology*. Michigan: University of Michigan Press.

Sahlins, Marshall. 1960 (1988). Evolution: specific and general. In *Evolution and Culture*, edited by M. Sahlins and E. Service. Ann Arbor: University of Michigan Press.

Sault, Nichole L. 1995. Many Mothers, Many Fathers: The Meaning of Parenting Around the World. Paper read at Ethics, Public Policy, and the Future of the Family, at Santa Clara University.

Schaffer, H.R., and P.E. Emerson. 1964. The development of social attachments in infancy. *Monographs of Social Research in Child Development* 29.

Schapera, Isaac. 1950. Kinship and Marriage among the Tswana. In *African Systems of Kinship and Marriage*, edited by A. R. Radcliffe-Brown and C. D. Forde. London: OUP for the International African Institute.

Scheffler, Harold W. 1973. Kinship, descent, and alliance. In *Handbook of Social and Cultural Anthropology*, edited by J. J. Honigman. Chicago: Rand McNally.

———. 2001. *Filiation and affiliation*. Boulder, CO: Westview Press.

Scheffler, Harold W., and Floyd G. Lounsbury. 1971. *A study in structural semantics : the Sirionо kinship system*. Englewood Cliffs: Prentice-Hall.

Schneider, D. 1965. Some Muddles in the Models: Or How the System Really Works. In *The Relevance of Models for Social Anthropology*, edited by M. Banton. London: Tavistock.

———. 1984. *A critique of the study of kinship*. Ann Arbor: University of Michigan Press.

Schneider, David Murray. 1968. *American kinship: a cultural account*, *Anthropology of modern societies series*. Englewood Cliffs, N.J.: Prentice-Hall.

———. 1972. What is Kinship all About. In *Kinship Studies in the Morgan Centennial Year*, edited by P. Reining. Washington: Anthropological Society of Washington.

———. 1980. *American kinship: a cultural account*. Second edition, *Anthropology of modern societies series*. Englewood Cliffs, N.J.: Prentice-Hall.

———. 1984. *A critique of the study of kinship*. Ann Arbor: University of Michigan Press.

Schneider, David Murray, and Richard Handler. 1995. *Schneider on Schneider : the conversion of the Jews and other anthropological stories*. Durham, N.C: Duke University Press.

Schrauwers, A. 1999. Negotiating parentage: the political economy of "kinship" in central Sulawesi, Indonesia. *American Ethnologist* 26 (2):310-323.

Schweitzer, Peter P. 2000. *Dividends of kinship: meanings and uses of social relatedness*. New York: Routledge.

Sherman, P. W. 1980. The limits of ground squirrel nepotism. In *Sociobiology: beyond nature/nurture?*, edited by G. W. Barlow and J. Silverberg. Boulder, Colorado: Westview Press.

———. 1981. Kinship, Demography, and Belding's Ground Squirrel Nepotism. *Behavioral Ecology and Sociobiology* 8:251-259.

Sherman, Paul W., Hudson K. Reeve, and David W. Pfennig. 1997. Recognition Systems. In *Behavioural Ecology*, edited by J. R. Krebs and N. B. Davies. Oxford: Blackwell Scientific.

Shibao, H. 1999. Lack of kin discrimination in the eusocial aphid Pseudoregma bambucicola (Homoptera : Aphididae). *Journal of Ethology* 17 (1):17-24.

Sigling, H. O., H. van Engeland, W. H. Gispen, and B. M. Spruijt. 1998. Attachment in rat pups, an experimental approach. *Neuroscience Research Communications* 23 (3):169-179.

Silk, J. B., R. M. Seyfarth, and D. L. Cheney. 1999. The structure of social relationships among female savannah baboons in Moremi Reserve, Botswana. *Behaviour* 136:679-703.

Silk, J.B. 1987. Adoption Among the Inuit. *Ethos* 15 (3):320-330.

———. 2001. Ties that Bond: The Role of Kinship in Primate Societies. In *New Directions in Anthropological Kinship*, edited by L. Stone. Oxford: Rowman and Littlefield.

Simmel, Georg. 1997 [1910]. Sociology of the Meal. In *Simmel on Culture*, edited by D. Frisby and M. Featherstone. London: Sage Publications.

Slocum, Sally. 1975 (1971). *Woman the Gatherer: Male Bias in Anthropology*. Edited by R. R. Reiter, *Toward an anthropology of women*. New York: Monthly Review Press.

Smuts, B. B. 1985. *Sex and Friendship in Baboons*. Chicago: Aldine.

Sober, E. and D.S. Wilson. 1998. *Unto Others: The Evolution And Psychology of Unselfish Behavior*. Cambridge, Mass: Harvard University Press

Spiro, Melford E. 1977. *Kinship and marriage in Burma: a cultural and psychodynamic analysis*. Berkeley: University of California Press.

Stafford, Charles Lester. 2000. Chinese patriliny and the cycles of *yang* and *laiwang*. In *Cultures of relatedness: new approaches to the study of kinship*, edited by J. Carsten. Cambridge: CUP.

———. 2000. *Separation and reunion in modern China*. Cambridge: CUP.

Stearns, S.C. 1992. *The evolution of life histories*. Oxford: OUP.

Stone, L. 1997. *Kinship, sex and gender*. Boulder, Colorado: Westview Press.

Stookey, J. M., and H. W. Gonyou. 1998. Recognition in swine: recognition through familiarity or genetic relatedness? *Applied Animal Behaviour Science* 55 (3-4):291-305.

Storrie, Robert. 2003. Equivalence, personhood and relationality: Processes of relatedness among the Hoti of Venezuelan Guiana. *Journal of the Royal Anthropological Institute* 9 (3):407-428.

Strathern, Andrew. 1973. Kinship, Descent and Locality: Some New Guinea Examples. In *The character of kinship*, edited by J. Goody. London: CUP.

Strathern, Marilyn. 1992. *After nature: English kinship in the late twentieth century*. Cambridge: CUP.

Stuart, R. J. 1991. Kin Recognition as a Functional Concept. *Animal Behaviour* 41:1093-1094.

Sugiyama, Y. 1965. On the social change of Hanuman langurs (*Presbytis entellus*) in their natural condition. *Primates* 6:381-418.

Summers, K., and R. Symula. 2001. Cannibalism and kin discrimination in tadpoles of the Amazonian poison frog, Dendrobates ventrimaculatus, in the field. *Herpetological Journal* 11 (1):17-21.

Sun, L. X., and D. Müller-Schwarze. 1997. Sibling recognition in the beaver: a field test for phenotype matching. *Animal Behaviour* 54:493-502.

Swartz, Karyl B., and Leonard A. Rosenblum. 1981. The Social Context of Parental Behavior: A Perspective on Primate Socialization. In *Parental Care in Mammals*, edited by D. J. Gubernick and Klopfer. New York: Plenum.

Symons, Donald. 1989. A Critique of Darwinian Anthropology. *Ethology and Sociobiology* 10:131-144.

———. 1992. On the Use and Misuse of Darwinism in the Study of Human Behaviour. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, edited by J. H. Barkow, L. Cosmides and J. Tooby. New York: OUP.

Tai, F. D., T. Z. Wang, and Y. J. Zhao. 2000. Inbreeding avoidance and mate choice in the mandarin vole (Microtus mandarinus). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78 (12):2119-2125.

Tang-Martinez, Z. 2001. The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behavioural Processes* 53:21-40.

Temrin, Hans, Susanne Buchmayer, and Magnus Enquist. 2000. Step-parents and infanticide: new data contradict evolutionary predictions. *Proc. Roy. Soc. Lond. B* 267:943-945.

Terrell, John, and Judith Modell. 1994. Anthropology and Adoption. *American Anthropologist* 96 (1):155-161.

Thomas, Philip. 1999. No substance, no kinship? Procreation, Performativity and Temanambondro parent/child relations. In *Conceiving persons : ethnographies of procreation, fertility, and growth*, edited by P. Loizos and P. Heady. New Brunswick, NJ: Athlone Press.

Thornhill, R., and N. Thornhill. 1985. Matriliny and sexual selection and conflict. *The Behavioural and Brain Sciences* 8 (4):679-680.

Tinbergen, Nikko. 1951. *The Study of Instinct*. Oxford: OUP.

Tooby, John, and Leda Cosmides. 1992. The Psychological Foundations of Culture. In *The Adapted Mind*, edited by J. Barkow. New York: OUP.

Topal, J., A. Miklosi, V. Csanyi, and A. Doka. 1998. Attachment behavior in dogs (Canis familiaris): A new application of Ainsworth's (1969) Strange Situation Test. Journal of Comparative Psychology 112 (3):219-229.

Toren, C. 1999. Compassion for one another: constituting kinship as intentionality in Fiji. Journal of the Royal Anthropological Institute 5 (2): 265-280.

Travis, J. M. J. 2001. The color of noise and the evolution of dispersal. *Ecological Research* 16 (1):157-163.

Trivers, Robert L. 1971. The Evolution of Reciprocal Altruism. *Quarterly Review of Biology* 46:35-57.

———. 1972. Parental Investment and Sexual Selection. In *Sexual Selection and the Descent of Man 1871-1971*, edited by B. Campbell. London: Heinemann.

———. 1974. Parent-Offspring Conflict. *American Zoologist* 14:249-264.

Tronick, Edward Z., Steve Winn, and Gilda A. Morelli. 1985. Multiple Caregiving in the Context of Human Evolution: Why Don't the Efe Know the Western Prescription for Child Care? In *The Psychobiology of Attachment and Separation*, edited by M. Reite and T. Field. London: Academic Press.

Turner, Bryan S., ed. 1998. *Readings in the anthropology and sociology of family and kinship*. Vol. 1, *The early sociology of the family*. London: Routledge/Thoemmes Press.

Tylor, E. B. 1889. On a Method of Investigating the Development of Institutions: applied to Laws of Marriage and Descent. *Journal of the Anthropological Institute of Great Britain and Ireland* 18:245-269.

Valsecchi, P., E. Choleris, A. Moles, G. Guo, and M. Mainardi. 1996. Kinship and familiarity as factors affecting social transfer of food preferences in adult Mongolian gerbils (Meriones unguiculatus). *Journal of Comparative Psychology* 110 (3):243-251.

van Gennep, Arnold. 1960 [1908]. *The rites of passage*. Translated by M. B. Vizedom and G. L. Caffee. London: University of Chicago Press.

van Schaik, C. P. 1996. Social evolution in Primates: the role of ecological factors and male behaviour. *Proceedings of the British Academy* 88:9-31.

———. 2000. Social counterstrategies against infanticide by males in primates and other mammals. In *Primate Males*, edited by P. M. Kappeler. Cambridge: CUP.

Vilaca, A. 2002. Making kin out of others in Amazonia. *Journal of the Royal Anthropological Institute* 8 (2):347-365.

Waldman, B. 1988. The Ecology of Kin Recognition. *Annual Review of Ecology and Systematics* 19:543-571.

Walls, S. C., and A. R. Blaustein. 1995. Larval Marbled Salamanders, Ambystoma-Opacum, Eat Their Kin. *Animal Behaviour* 50:537-545.

Walls, S. C., C. S. Conrad, M. L. Murillo, and A. R. Blaustein. 1996. Agonistic behaviour in larvae of the northwestern salamander (Ambystoma gracile): The effects of kinship, familiarity and population source. *Behaviour* 133:965-984.

Walters, J. 1987. Kin Recognition in Non-human Primates. In *Kin recognition in animals*, edited by D. J. C. Fletcher and C. D. Michener. New York: Wiley.

Washburn, Sherwood. 1951. The analysis of primate evolution with particular reference to the origin of man. In *Cold Spring Harbor Symposia on Quantitative Biology*. New York.

Watson, J.B. 1983. *Tairora Culture: Contingency and Pragmatism*. Seattle: University of Washington Press.

Weismantel, Mary. 1988. *Food, Gender and Poverty in the Ecuadorian Andes*. Philadelphia: University of Pennsylvania Press.

———. 1995. Making kin: kinship theory and Zumbagua adoptions. *American Ethnologist* 22 (4):685-709.

Weiss, Robert S. 1991. The attachment bond in childhood and adulthood. In *Attachment across the Lifecycle*, edited by C. Murray-Parkes, J. Stevenson-Hinde and P. Marris. London: Routledge.

Westermarck, Edward. 1891. *The history of human marriage*. London: Macmillan.

Widdig, A., P. Nurnberg, M. Krawczak, W. J. Streich, and F. Bercovitch. 2002. Affiliation and aggression among adult female rhesus macaques: A genetic analysis of paternal cohorts. *Behaviour* 139:371-391.

Widdig, A., P. Nurnberg, M. Krawczak, W. J. Streich, and F. B. Bercovitch. 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences of the United States of America* 98 (24):13769-13773.

Wigglesworth, V.B. 1964. *The Life of Insects*. New York: Mentor Books.

Williams, George C. 1966. *Adaptation and natural selection : a critique of some current evolutionary thought*. Princeton: Princeton University Press.

Williams, George C. 1993. Mother Nature is a Wicked Old Witch. In *Evolutionary Ethics*, edited by M. H. Nitecki and D.V. Nitecki. Albany: State University of New York.

Wilson, Edward Osborne. 1975. *Sociobiology : the new synthesis*. Cambridge, Mass: Belknap Press of Harvard University Press.

Wilson, D.S. and E. Sober. 1994. Reintroducing group selection to the human behavioral sciences. Behavioral and Brain Sciences 17 (4): 585-654.

Witherspoon, Gary. 1975. Navajo kinship and marriage. Chicago: University of Chicago Press.

Wolff, J. O. 1992. Parents Suppress Reproduction and Stimulate Dispersal in Opposite-Sex Juvenile White-Footed Mice. *Nature* 359 (6394):409-410.

Wrangham, Richard W., and Dan I. Rubenstein. 1986. Social Evolution in Birds and Mammals In *Ecological Aspects of Social Evolution*, edited by R. W. Wrangham and D. I. Rubenstein. Princeton, NJ: Princeton University Press.

Wrangham, Richard W. 1986. Ecology and Social Relationships in Two Species of Chimpanzee. In *Ecological Aspects of Social Evolution*, edited by R. W. Wrangham and D. I. Rubenstein. Princeton, NJ: Princeton University Press.

Wright, S. 1948. Genetics of Populations. In *Encyclopaedia Britannica*. London.

Wright, Sewall. 1922. Coefficients of Inbreeding and Relationship. *The American Naturalist*:330-338.

Yamagiwa, J. 1999. Socioecological factors influencing population structure of gorillas and chimpanzees. *Primates* 40 (1):87-104.

Yanagisako, Sylvia Junko, and Jane Fishburne Collier. 1987. Towards a Unified Analysis of Gender and Kinship. In *Gender and kinship: essays toward a unified analysis*, edited by J. F. Collier and S. J. Yanagisako. Stanford, Calif.: Stanford University Press.

Young, Michael Dunlop, and Peter Willmott. 1957. *Family and kinship in East London*, *Reports of the Institute of Community Studies*. London: Routledge & Kegan Paul.

Zahn-Waxler, C. 1991. The Case for Empathy: A Developmental Perspective. *Psychological Inquiry* 2 (2):155-158.

Zihlman, Adrienne L. 1981. Women as Shapers of the Human Adaptation. In *Woman the Gatherer*, edited by F. Dahlberg. London: Yale University Press.

———. 1993. Sex differences and gender hierarchies among primates: an evolutionary perspective. In *Sex and gender hierarchies*, edited by B. D. Miller. Cambridge: CUP.

Zimmer-Tamakoshi, Laura. 2001. Development and Ancestral Gerrymandering: Schneider in Papua New Guinea. In *The cultural analysis of kinship : the legacy of David M. Schneider*, edited by R. Feinberg and M. Ottenheimer. Urbana: University of Illinois Press

INDEX: