Cambridge University Press
0521017556 - Kin Recognition
Edited by Peter G. Hepper
Excerpt
More information

# Introduction

Peter G. Hepper

The importance of kinship for human societies has long been recognized, indeed the interest in kinship is reflected in the large number of works, plays, books, operas, etc., which have kinship, often mistaken, as their central theme. Whilst there has been little doubt that humans recognize their kin and respond differentially to them, the ability of animals to recognize and respond differentially to kin has received little attention. In recent years, however, study of the influence of kinship on the social behaviour of animals has increased dramatically. Much of the impetus for this research can be attributed to the seminal works of Hamilton (1964a,b) and later Wilson (1975). Evidence that kinship, or genetic relatedness, influences an individual's behaviour has now been documented in all the major groups of animals – from single-celled organisms (e.g. Grosberg & Quinn, 1986) to man (e.g. see Porter, this volume). Reptiles remain an exception to this and only recently have studies appeared providing evidence of kin recognition in this group (e.g. Werner *et al.*, 1987), which probably reflects a lack of empirical investigation rather than a lack of ability to recognize kin. As diverse as the groups of animals which exhibit evidence of kin recognition are the behaviours in which individuals respond differentially on the basis of kinship; colonization patterns, mating, play, aggression, feeding, schooling, swarming, defence, etc. all are influenced by kinship. Investigations of the ability to recognize kin have revealed that individuals have well developed capabilities to recognize kin; siblings, half-siblings, cousins, parents, offspring, grandparents, aunts and uncles are all capable of being discriminated. Kinship thus appears to influence behaviour throughout the animal kingdom.

The theoretical importance of kinship for behaviour derives from the concept of inclusive fitness outlined by Hamilton (1964a,b; see Grafen, 1984 for full discussion). Essentially Hamilton argued that since related individuals have a number of genes in common that are identical by descent, an individual may pass on its genes to the next generation via its relations. Thus, an individual's fitness, its *inclusive fitness*, should include its own reproductive success (not including that due to the actions of others) *and* the reproductive success of related conspecifics arising as a result of its actions. Thus, by responding differentially to kin and non-kin, an individual may achieve greater gains in fitness than individuals unable to do so. Mate choice and optimal outbreeding (e.g. Bateson, 1983) provide a further reason for expecting kinship to exert an effect on behaviour. The long established disadvantages of inbreeding and the more recently established problems of extreme outbreeding indicate that kinship may play an important role in the choice of a mate. It may, therefore, be expected that individuals would respond differentially to kin and non-kin, an expectation that is supported by empirical observations. To achieve this, individuals may be expected to have some means of recognizing their kin. The study of how individuals recognize their kin received little attention until the late 1970s. Whilst investigations assessed whether individuals responded differently to kin and non-kin, little attention was paid to the question of how individuals achieved this. One major exception, however, is the field of parent-offspring recognition where this ability had long been studied in a variety of species.

Kin recognition may be divided into two broad areas, the exhibition of differential behaviour to kin and non-kin, referred to as *kin discrimination*, and the mechanisms used to identify individuals as kin, non-kin, or a particular degree of relatedness, referred to as *kin recognition*. A distinction between the two is important because logically inferences drawn from results in one area may not provide information about the other. Thus, individuals who do not respond differentially to kin and non-kin, i.e. show no *kin discrimination*, may be unable to recognize kin, alternatively they may be perfectly well able to recognize kin but do not exhibit a discrimination in this situation. No *kin discrimination* need not imply no *kin recognition*. This places the emphasis squarely on the researcher and the methodology used to demonstrate that the animal in question can recognize its kin rather than simply relying on the animal to show that it can recognize its kin. More recently concern has been expressed as to whether evidence of kin discrimination is a result of kin recognition. Particular concern has been expressed over kin bias in mate choice where this may not necessarily be the result of kin recognition (see Barnard and Aldhous, this volume). Thus, it is important to distinguish between *kin discrimination* and *kin recognition*. A variety of other terms are used in the kinship literature and because of differences in their use by various authors no attempt has been made to provide a standard glossary of terminology in this book. Readers are referred to the definitions provided by each author.

Over the years, research has successfully demonstrated the ability of individual organisms to recognize their kin and to discriminate between kin

Cambridge University Press
0521017556 - Kin Recognition
Edited by Peter G. Hepper
Excerpt
More information

and non-kin. The importance of kinship in the individual's behaviour and its prevalence throughout the animal kingdom is, therefore, not in question. More recently, a more critical appraisal of kinship and behaviour has been undertaken and both the evidence for discriminative responding and the ability of individuals to recognize their kin has been subject to detailed examination. It is the aim of this volume to consider these recent developments. Each chapter in the volume concentrates on a particular theme and although often illustrated with reference to a particular taxonomic group, the considerations discussed should apply to all animal groups. Very broadly the first part of the book deals with kin discrimination and the second with kin recognition.

Although it is often taken for granted that animals do exhibit kin discrimination, the first part of this volume examines the evidence for this and considers the situations in which kinship can be expected to exert an effect. The strongest evidence of differential responsiveness to kin and non-kin has often been thought to be provided by the non-human primates. Perhaps because of their close similarity with man, for whom kinship plays an important role, primates of all animal groups were expected to exhibit evidence of kin discrimination. Poor methodology and inappropriate analysis however have raised questions regarding the evidence of kin discrimination in primates. The chapter by Bernstein assesses the evidence for kinship influences on behaviour in the non-human primates. The following chapter by Ligon deals with co-operation and reciprocity in birds and mammals. Co-operation is common both to human and animal behaviour, it is often highly developed and is clearly frequently found in the animal kingdom. However, such behaviour may not require kinship for its maintenance and the role of kinship in co-operative behaviour is critically assessed by Ligon. As has often been pointed out, the complex societies of ants, wasps and bees pose special problems for Darwin's evolutionary theory. Jaisson discusses, with examples from the ants and wasps, how these can be overcome by reference to kinship and the 'superorganism' concept and illustrates the behavioural mechanisms used in colonies of ants and wasps to recognize their kin. The costs of recognizing kin are considered by Beecher using the example of parent–offspring recognition. It is often overlooked that recognizing kin and being recognized as kin involves costs, e.g. being identified as non-kin may result in rejection, increased aggression, etc. This chapter considers how the costs of kin recognition and discrimination will influence the evolution and development of kin recognition systems. Kinship has often been proposed as a factor in determining mate choice, however, Barnard and Aldhous discuss how kin bias in mating behaviour may have arisen for reasons that are unrelated to kinship. This chapter serves as a timely reminder that caution should be exerted in ascribing kin bias to kin discrimination. The genetic structure which has received most attention in studies of kin recognition is that of the major histocompatibility complex (MHC), which has been implicated in recognition in both invertebrates and vertebrates. The chapter by Boyse, Beauchamp, Yamazaki and Bard, reviews studies of the MHC concentrating on its role in influencing mating preferences and the production of the individual's odour signature. The kin recognition capabilities of amphibians are well understood but questions have been raised as to the functional significance of kin recognition for this group. Waldman examines the possible functions of this ability for amphibians.

Studies of how individuals recognize conspecifics have been criticized (e.g. Hepper, 1986) for providing little detail of how these processes take place. The second part of this volume examines research attempting to elucidate how individuals recognize their kin. In order to be recognized as kin, individuals must have some cue which signifies them as kin. The cues of kin recognition are the subject of the chapter by Halpin, where the information content, the origins and the sensory modality of cues used in the recognition of kin are discussed. Hepper discusses an approach which can be better used to determine how individuals recognize their kin. This approach enables the underlying basis of kin recognition, especially its development and how and where cues of kinship are classified, to be better understood. The chapter demonstrates that there are a wide variety of means available to the individual to enable it to recognize its kin. The motivational state of the individual has often been overlooked in the study of kin recognition yet this may play an important role in identifying kin. The fact that fathers enter a paternal state and refrain from killing their own young is discussed by Elwood detailing how the individual's state can be used to recognize kin. The possibility that the female may use this to deceive the male is also considered. Most studies of kin recognition have concluded that individuals have to learn about their kin in order to recognize them and, therefore, have to ensure that the information they learn is from related individuals. One means of ensuring that individuals learn about their kin is to start learning before birth. This, however, requires a certain level of sophistication in the sensory and learning capabilities as well as information regarding kinship being available to the fetus. This is the subject dealt with by Robinson and Smotherman. Underlying the ability to recognize is some neural process which converts the perceived cue to a measure of relatedness. For most species little is known about these processes. However, in one case, that of imprinting, the underlying neural processes are being elucidated. The chapter by Johnson examines what is known about the underlying physiological basis to imprinting and concentrates upon the role of the intermediate and medial parts of the hyperstriatum ventrale. Given the many factors involved in recognizing kin, the construction of a kin recognition system can be expected to be somewhat complex. Yet Getz, using the honey bee as his example, proposes a kin recognition model for this animal and reviews the evidence for recognition in the bee. The final chapter returns to humans. For so long kinship has been acknowledged to play an important role in human societies yet very little is known about how recognition is achieved. Porter, concentrating on the mother–infant dyad, examines the development and sensory mediation of kin recognition and its adaptive significance for this dyad.

Kin recognition encompasses a wide diversity to topics from the nepotistic aiding behaviour of certain primates to the neural processes involved in classifying individuals as kin. The aim of this book is to bring together a collection of papers that illustrate the breadth of the area as well as providing critical analysis of topics within the area. There is no doubt that the study of kin recognition is exciting. The fact that a wide range of species (from single-celled organisms to man) appear to exhibit the same complex patterns of behaviour is fascinating and prompts many questions. Also this book has aimed to provide an insight into the many questions currently being asked to understand the individual's ability to recognize its kin.

## References

Bateson, P. P. G. (1983). Optimal outbreeding. In *Mate Choice*, ed. P. P. G. Bateson, pp. 257–277. Cambridge: Cambridge University Press.

Grafen, A. (1984). Natural selection, kin selection and group selection. In *Behavioural Ecology*, ed. J. R. Krebs & N. B. Davies, pp. 62–4. Oxford: Blackwell.

Grosberg, R. K. & Quinn, J. F. (1986). The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature*, **322**, 456–9.

Hamilton, W. D. (1964a). The genetical evolution of social behaviour I. *J. Theor. Biol.*, **7**, 1–16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour II. *J. Theor. Biol.*, **7**, 17–52.

Hepper, P. G. (1986a). Kin recognition: functions and mechanisms. A review. *Biol. Rev.*, **61**, 63–93.

Werner, D. I., Baker, E.M., Gonzalez, E. del C., Sosa, I.R. (1987). Kinship recognition and grouping in hatchling green iguanas. *Behav. Ecol. Sociobiol.*, **21**, 83–9.

Wilson, E. O. 1975. *Sociobiology*. Cambridge, MA: Belknap Press.

CAMBRIDGE

Cambridge University Press
0521017556 - Kin Recognition
Edited by Peter G. Hepper
Excerpt
More information

# 1

# The correlation between kinship and behaviour in non-human primates

Irwin S. Bernstein

In 1986 Carolyn Ehardt and I published a paper, ‘The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*)’. The title of this paper is not unusual; it asserts that kinship is an independent variable that influences aggressive behaviour, as a dependent variable. This suggests that manipulation of the first will alter the second. Naturally we would be quick to deny a causal relationship and would repeat that science only demonstrates correlations, not causation. But why then did we not title the paper, ‘The influence of aggressive behaviour on kinship’? If we had done so, many would have quickly pointed to this as an example of a backward causal argument. In fact, despite our denials, we do attempt to suggest causal relationships in our correlations and, in this case, as in many others, there is a clear correlation between two variables but there may be no direct causal relationship.

Perhaps we have acknowledged the contributions of Tinbergen (1951) only to fail to apply them to our own thinking. All too often we confuse function with proximal cause, evolutionary cause, and even structure (as in definitions like ‘the process leading to’). Functional outcomes are argued to be the motivational cause of behaviour (the animal was ‘trying to drive the predator away’) and if something functions in an adaptive fashion we often assume that this is because it was selected for this function during evolution (birds developed wings in order to fly south in the winter). Teleological reasoning can be very seductive, whether we are looking for the cause of behaviour by examining the consequences, or we are looking for the answer to questions about evolutionary processes by searching for an adaptive explanation for observed behaviour.

Ever since Wilson (1975) published *Sociobiology*: *The New Synthesis* and called our attention to Hamilton’s paper (1964) on inclusive fitness theory, we have been keenly aware of the selective pressures that would favour individuals that selectively benefited kin, at a cost to themselves less than the benefit received by their kin, devalued by the degree of relatedness. Degree of relatedness is often equated with kinship but, in fact, these terms are not synonymous. Even disregarding human kinship terms used for genetically unrelated people (your mother's sister's husband is your 'uncle') unrelated individuals do not necessarily have zero genes in common, nor do cousins necessarily share only half as many genes in common as do aunt and nephew. It is true, on average, for genes identical by descent from a common grandparent, but how many genes are shared in common by members of a population of the same species? When we measure degree of inbreeding we typically examine only those loci known to be heterogeneous in the population and regard as uninteresting loci that show no variation. Moreover, if there are three alleles for human ABO blood groups, then do we regard as 'kin', of some degree, all of those who share the same phenotype as our own and therefore share one or both alleles in common with ourself? If we could trace back far enough would we find that we were both carrying the same alleles derived from common ancestors, albeit very distant ancestors?

Kinship discussions are often marred by facile assumptions that degree of genetic relatedness and degree of kinship are synonymous, where kinship is defined as counting the number of links back to a common ancestor. When we use kinship in the second sense, then surely only humans determine kinship by counting generations to a common ancestor. All other animals must use some other criteria that correlates with this measure, or show no correlation between kinship and behaviour. In inbred strains we might expect considerable differences in the degree to which kinship influenced behaviour, if one strain literally could measure the proportion of genes in common whereas the other strain responded differentially to others based on association with the same mother, and the associates of that mother.

The actual pattern of correlations between behaviour and kinship, phenotypic factors and experiential factors may tell us much more about mechanism than any number of postulated possible mechanisms. The mere fact that all individuals, not genetically identical, are unique phenotypes does not mean that degrees of phenotypic variation are related one to one with genetic relatedness. We may recognize each individual as having unique dermatoglyphics, voice signature, visible anatomical properties, retinal patterns and chemical properties. We may succeed in recognizing similarities among some individuals and may be able to develop a classification scheme based on objective criteria. None of this is to say that our classification either has a direct genetic correlation, nor that individuals in a population actually respond to the variation that we recognize so easily. Even when it would be adaptive to do so, and obviously so easy to do from our perspective, the actual demonstration of the phenomena may be elusive.

As an analogy, I have often noted that rhesus monkeys treat members of the two sexes differently and that there is, what appears to be, extraordinary interest in the genitalia of infants on the part of adults. This is such an obvious sex identification procedure for humans that it seems almost foolish to ask if monkeys do indeed behave differently towards other monkeys based on the anatomical differences between males and females. Is it possible, however, that mothers respond towards their infants in accordance with the infants' behaviour and not their anatomy? Is it possible that monkeys respond primarily to the sexual differences in behaviour of males and females rather than to the differences in their anatomy? Is it possible that monkeys receive information on individual identity by examining all bodily orifices and chemical cues, and that data on sex and kinship are not obtained from these cues, even though it is theoretically possible to obtain such data from these cues? Is it possible that primates may fail to respond to cues that salmon, frogs and bees discriminate so keenly?

## Non-human primate behaviour and kinship correlations

Our first task must be to establish the existence of a phenomenon before we try to understand mechanism (cause), function, ontogeny and evolution. In this case, it is relatively easy to demonstrate a strong correlation between certain classes of kinship and a wide variety of primate behavioural patterns. In multiple primate taxa, individuals in physical proximity, or huddled together in the cold, or resting together, or in physical contact or actively engaged in social grooming, have all been found to be more likely to be kin than would be expected by chance (Sade, 1965; Ransom & Rowell, 1972; Vessey, 1973; Loy & Loy, 1974; Kurland, 1977; Mori, 1977; Cheney, 1978; Baxter & Fedigan, 1979; Ehardt & Bramblett, 1980; Hanby, 1980; Walters, 1980; Silk *et al.*, 1981; Berman, 1982; Silk, 1982, 1984; Takahata, 1982b; Furuichi, 1983; Giacoma, 1983; Baker & Estep, 1985; Colvin, 1985; Colvin & Tissier, 1985; Fairbanks & McGuire, 1985; Hornshaw, 1985; Koyama, 1985; Taylor & Sussman, 1985; Glick *et al.*, 1986a,b; Quiatt, 1986). Although most of the data are from Old World monkeys, particularly macaques and baboons, wherever substantial data on kinship and behaviour are available positive correlations, with maternal kinship at least, have been reported. The data for play and mounting behaviour show weaker correlations with kinship, but age and sex also strongly correlate with play and mounting behaviour and, for example, the availability of male peers among kin as play partners may only be likely in large matrilines (Dittus, 1979). Mounting behaviour is also strongly influenced by age, sex and familiarity, and this may account for observations reporting that older males mount their kin proportionately less often than do younger males (Glick *et al.*, 1986b; Ruehlmann *et al.*, 1987) rather than a maturational kinship effect *per se*.

'Altruistic' behaviour is difficult to explain in evolutionary terms unless it is directed primarily towards kin (in which case it is not altruistic as it is in the genetic interests of the individual to do so). Altruistic behaviour like food sharing, co-operation and alarm calling all appear to be strongly correlated with kinship. Cheney & Seyfarth (1980, 1985a,b) report that vervets (*Cercopithecus aethiops*) not only alarm call and respond to the alarm calls of others in a manner demonstrating clear kinship biases, but that unrelated females also will look towards the mother in response to the playback of an infant's distress vocalization. Moreover, Marler (1985) reports that there are differences in the structure of certain vocalizations when directed towards kin.

The clearest evidence of primates engaging in behaviour which benefits another at some risk and/or cost to themselves exists in the area of third party interferences in agonistic encounters. Although one might argue that joining a victor in attacking a defeated victim entails little risk, and in no way benefits the original aggressor, it may help the interfering animal to acquire status relative to the victim, or to establish a coalition with the aggressor. Individuals, however, will also come to the aid of victims against aggressors that have repeatedly defeated the aiding animal in the past. This second type of defence surely entails some risk to the interfering animal, and this type of agonistic interference correlates strongly with sex (females do more of it) and matrilineal kinship. Although males do much less aiding of kin than do females, and seldom will aid an individual against an opponent who is dominant to them, the few times a male does so is almost always in defence of his kin (Koford, 1963; Sade, 1965, 1968; Kaplan, 1976, 1977, 1978; de Waal, 1977; Kurland, 1977; Massey, 1977; Lee & Oliver, 1979; Watanabe, 1979; Hardy, 1981; Bramblett, 1973; Datta, 1983a; Horrocks & Hunte, 1983a,b; Estrada, 1984; Seyfarth & Cheney, 1984; Bernstein & Ehardt, 1985; Colvin, 1985; Colvin & Tissier, 1985; Fairbanks & McGuire, 1985; Netto & Van Hooff, 1986; Reinhardt *et al.*, 1986). The decrease in aid of kin by males, as they become adult, is not matched by a decrease in the aid that natal adult males receive from kin. (Eaton, 1976).

The consequences of third party interferences in agonistic encounters goes beyond the immediate protection of the animal being aided. Kawai (1965) and Kawamura (1965) have proposed a theory of the social inheritance of dominance in primates and it has been demonstrated to predict social dominance relationships in several species (Koyama, 1967; Sade, 1969; Loy & Loy, 1974; Loy, 1975; Kawanaka, 1977; Dittus, 1979; Lee & Oliver, 1979; Cheney & Seyfarth, 1980; Walters, 1980; Cheney, *et al.*, 1981; Datta, 1983a,b; Horrocks & Hunte, 1983a,b). Predictions based on the theory (Chapais & Shulman, 1980) are sometimes contradicted by data (Missakian, 1972; Angst, 1975; Chikazawa *et al.*, 1979; Hrdy, 1981; Hausfater *et al.*, 1982; Chapais, 1985; Paul & Kuester, 1987), but it seems clear that dominance relationships among females, in at least some species, are strongly influenced

Cambridge University Press
0521017556 - Kin Recognition
Edited by Peter G. Hepper
Excerpt
More information

by patterns of third party interference in agonistic encounters. Mothers are particularly likely to aid their offspring, but other matrilineal kin can also play important roles. In those cases where a young adult female comes from a matriline that was overthrown by one or more other matrilines after her birth, the female does not achieve the rank of her mother at the time of her birth (Ehardt & Bernstein, 1986). It seems essential for a young female to have at least one living matrilineal relative that has retained high rank, and will come to her aid, for a female to acquire the rank predicted at her birth (Chapais, 1985). If a female's family has not been overthrown, on the other hand, even an orphan female may rise to her mother's former rank with the aid of one or more others willing to support her (Altmann, 1980; Walters, 1980).

## Aggression and kinship

The data reported so far indicate that animals behave towards matrilineal kin in ways that may reasonably be presumed to benefit the recipients of the behaviour. Such correlations are readily accommodated by inclusive fitness theory relating selective pressures to the genetic concomitants of the behaviour. In order to accommodate data on aggression and kinship to evolutionary theory so facilely, we would need to demonstrate a negative correlation between aggressive targets and genetic relatedness. Whereas Silk *et al.*, (1981) have claimed that monkeys show less aggression towards their kin, the vast majority of the data indicates that animals receive far *more* aggression from their matrilineal kin than would be expected by chance. Moreover, it is the more severe forms of aggression involving physical contact which are the more strongly biased towards kin (Kurland, 1977; Horrocks & Hunte, 1983a; Niemeyer & Chamove, 1983; Colvin, 1985; Eaton *et al.*, 1985, 1986; Bernstein & Ehardt, 1986). Furuichi (1983) concluded that due to insufficient data, the hypothesis of reduced aggression towards kin is not tenable. Attempts to explain the data away by weighting the frequency of aggression received by time in proximity in no way nullifies the fact that individuals, especially younger animals, are most likely to receive the more consequential forms of aggression from their own kin. Mothers are particularly prone to bite their own infants, although such biting may subjectively appear to be inhibited (Bernstein & Ehardt, 1986). Walters (1987), in his review, examined the proximity explanation hypothesis and noted that it would also have to be applied to grooming and agonistic aiding, as well as aggression. He concluded, however, that even with a compensation for time in proximity, data for grooming, agonistic aiding and aggression remain significantly correlated with kinship.

Aggressive interactions may result from competitive conflicts which will arise most often among animals in close proximity, but aggression does not