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Review

Nepotistic cooperation in non-human primate groups

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Darwin was struck by the many similarities between humans and other primates and believed that these similarities were the product of common ancestry. He would be even more impressed by the similarities if he had known what we have learned about primates over the last 50 years. Genetic kinship has emerged as the primary organizing force in the evolution of primate social organization and the patterning of social behaviour in non-human primate groups. There are pronounced nepotistic biases across the primate order, from tiny grey mouse lemurs (*Microcebus murinus*) that forage alone at night but cluster with relatives to sleep during the day, to cooperatively breeding marmosets that rely on closely related helpers to rear their young, rhesus macaque (*Macaca mulatta*) females who acquire their mother's rank and form strict matrilineal dominance hierarchies, male howler monkeys that help their sons maintain access to groups of females and male chimpanzees (*Pan troglodytes*) that form lasting relationships with their brothers. As more evidence of nepotism has accumulated, important questions about the evolutionary processes underlying these kin biases have been raised. Although kin selection predicts that altruism will be biased in favour of relatives, it is difficult to assess whether primates actually conform to predictions derived from Hamilton's rule: $br > c$. In addition, other mechanisms, including contingent reciprocity and mutualism, could contribute to the nepotistic biases observed in non-human primate groups. There are good reasons to suspect that these processes may complement the effects of kin selection and amplify the extent of nepotistic biases in behaviour.

Keywords: kin selection; cooperation; kin recognition; primate; altruism

1. INTRODUCTION

In 1838, Charles Darwin made the acquaintance of Jenny, the first orangutan exhibited in England. His visits with Jenny at the Regents Park Zoo in London made a deep impression on him: 'Let man visit Ouranoutang in domestication, hear its expressive whine, see its intelligence when spoken [to]; as if it understands every word said—see its affection. —to those it knew. —see its passion & rage, sulkiness, & very actions of despair; . . . and then let him boast of his proud preeminence. . . Man in his arrogance thinks himself a great work, worthy the interposition of a deity. More humble and I believe true to consider him created from animals'. Others were also struck by the similarities between humans and apes. When Queen Victoria contemplated Jenny's replacement and namesake in May 1842, she found her '. . . frightful, and painfully and disagreeably human'.

Darwin believed that the similarity between apes and humans was the consequence of shared ancestry, but so little was known about the origin and behaviour of apes and other primates that he did not appreciate the full extent of the connections between humans and other primates. Today, 170 years after Darwin

first met Jenny, we have a firm understanding of the phylogenetic relationships between ourselves and other primates, and we have accumulated a large body of information about the social behaviour of the diverse members of the primate order. Biological kinship has emerged as a primary organizing force in the evolution of primate social organization and the patterning of social behaviour within primate groups. Had Darwin known that other primates distinguish kin from non-kin, form enduring relationships with their offspring, selectively groom, support and reconcile conflicts with their relatives and are aware of the kinship relationships between other group members, he would have been even more certain of the deep evolutionary links between humans and other animals.

The first clue about the role of biological kinship in primate groups emerged from studies of indigenous populations of Japanese macaques (*Macaca fuscata*). Imanishi and his co-workers were the first to systematically monitor the behaviour of known (and named) individuals and to conduct continuous, long-term observations of social groups (Matsuzawa & McGrew 2008). These observations allowed them to construct dominance hierarchies for both sexes and to construct matrilineal geneologies. This led to the discovery that females acquire their mothers' dominance ranks (Kawai 1958; Kawamura 1958). These findings were complemented by pioneering observations of the behaviour of rhesus macaques (*Macaca mulatta*) on

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Cayo Santiago Island, which documented strong and enduring maternal kin biases in association, tolerance, grooming and play in rhesus macaques (Rawlins & Kessler 1986).

But it was not until the publication of Wilson's (1975) *Sociobiology: the new synthesis* that primatologists linked these empirical findings about nepotistic biases in social behaviour to kin selection theory (Kurland 1977). Then, primatologists began to focus on the role of kin selection in the distribution of altruistic behaviours, such as grooming and support, in primate groups (Chapais & Berman 2004), and the logic of kin selection was integrated into socioecological models of the evolution of primate social organization (Wrangham 1980; van Schaik 1983; Sterck *et al.* 1997; Isbell & Young 2002).

In this paper, I review what we have learned about the mechanisms underlying kin recognition and the nature and extent of kin biases in behaviour in primates. I use primate social organization as the organizing framework for the review of nepotistic biases in behaviour because the size and composition of social groups influence the availability of kin and the potential for kin biases in behaviour to develop. We know much more about the effects of maternal relatedness on the distribution of altruistic behaviour than we do about the effects of paternal relatedness because of uncertainties about the paternity of infants born in multi-male groups. In addition, research effort has not been evenly distributed across the primate order so we know much more about the behavioural strategies of some Old World monkeys and apes than we do about most New World primates or prosimians.

2. KIN RECOGNITION MECHANISMS

In order for kin selection (Hamilton 1964) to favour the evolution of altruistic behaviour, animals must direct altruism selectively to relatives. Hamilton (1987) predicted that the ability to identify kin would be most fully developed in species that live in social groups; when there are opportunities for costly behaviours, such as egg dumping or infanticide; and when passive, context-dependent mechanisms for distinguishing kin from non-kin are not likely to be effective. Primates clearly fit these three conditions. Most primates live in large and relatively stable social groups (Smuts *et al.* 1987). Even the most solitary primates such as orangutans and galagos have regular interactions with familiar conspecifics (Galdikas 1988; Nash 2004). Primates engage in a variety of fitness-reducing behaviours, including severe intragroup aggression and infanticide (van Schaik & Janson 2000). Finally, most primates live for extended periods of time in groups that include both relatives and non-relatives, so context-driven mechanisms for distinguishing kin are likely to be of limited use.

(a) *Familiarity*

Close association early in life is generally thought to be the primary basis for kin recognition in mammalian groups (Holmes & Sherman 1983), including primates (Bernstein 1991; Rendall 2004). In most species of monkeys and apes, infants remain in constant contact with their mothers during the first few weeks of life.

Mothers nurse, nuzzle and inspect their newborns and are thought to learn to recognize their smell, voice or appearance during the first few weeks of life. Similarly, infants may learn to recognize their mothers during this period. The importance of early familiarity is supported by the evidence that captive 'foster' mothers routinely accept strange infants, even when they are not the same sex, exact ages or species as their own infants (Deets & Harlow 1974; Bernstein 1991; Owren & Dieter 1989). Lasting associations between mothers and offspring may also provide opportunities for identifying other categories of maternal kin. Juveniles may see their mothers nursing younger offspring, providing cues about their relationship to siblings. Mothers may observe their adult daughters nursing their grandoffspring, and females may observe their sisters nursing nephews or nieces. Other behavioural cues such as high rates of association or grooming may enable young monkeys to identify their older siblings, aunts and grandmothers.

In some cases, group membership may provide reliable cues of kinship. In cooperatively breeding and pair-bonded species, most infants born in the group will be half or full siblings. However, extra-pair copulations may reduce relatedness among offspring to the level of half siblings.

Group membership and early association provide less information about paternal kinship than maternal kinship. In most primate species, females do not form extended associations with their mates, limiting infants' abilities to deduce their fathers' identity through associations with their mothers. Baboons may constitute an exception to this rule, as close associations between mothers of newborn infants and their former mating partners may provide reliable predictors of paternity (Buchan *et al.* 2003; Moscovice *et al.* 2009). Paternal kin recognition may also be based on consistent correlates of relatedness within primate groups. As Altmann (1979) originally pointed out, when a single male monopolizes mating opportunities within a group, age mates are likely to be paternal half siblings. Therefore, primates might use age similarity as a proxy for paternal relatedness. Genetic evidence indicates that there is considerable reproductive skew in many primate species, including species that normally live in multi-male groups (reviewed by Widdig 2007). Within the genus *Macaca*, the extent of male reproductive skew is associated with the nature of female–female relationships within groups. In species with the most reproductive skew, and presumably the highest levels of paternal relatedness, females have the most tolerant social relationships (Schülke & Ostner 2008). Thus, contextual cues such as age similarity may be reliably associated with paternal relatedness in a broad range of primate species.

(b) *Phenotypic cues*

Phenotypic cues such as odour, vocal qualities or physical appearance could all play a role in primate kin recognition systems (reviewed by Rendall 2004; Widdig 2007). Animals may detect phenotypic similarities between themselves and others or acquire a

template based on the phenotype of familiar relatives and use this template to identify other relatives (Holmes & Sherman 1983; Tang-Martinez 2001; Holmes & Mateo 2007). Odour, which is linked to variation in major histocompatability complex (MHC) alleles, plays an important role in kin recognition systems in some mammalian species. However, over the course of primate evolution, there has been a reduction of emphasis on olfaction and a concomitant increase in emphasis in vision. In macaques and chimpanzees (*Pan troglodytes*), approximately one-third of the olfactory receptor genes carry one or more coding gene disruptions and have become pseudogenes (Widdig 2007). In humans, over half of the analogous genes have become pseudogenes. Nonetheless, human mothers can recognize the odour of their own offspring, and humans can distinguish the odours of kin, friends and strangers (Weisfeld *et al.* 2003). In addition, women are attracted to the odour of men with human leucocyte antigen genes (equivalent to MHC) that are similar, but not identical, to their own (Jacob *et al.* 2002). This suggests that while monkeys and apes may have lost much of their olfactory acuity, olfactory cues could still play some role in their kin recognition systems.

Efforts to determine the role of phenotypic cues in primate kin recognition systems have generated mixed results. The first attempt to examine this question was conducted by Wu *et al.* (1980). They showed that young pig-tailed macaques (*Macaca nemestrina*), who were reared apart from all relatives, showed consistent preferences for unfamiliar half siblings over unfamiliar non-kin (matched for age and sex) on their first encounter. In these experiments, preferences were measured using differential rates of approaches and visual inspections of the unfamiliar monkeys. Later, Fredrickson & Sackett (1984) and Sackett & Fredrickson (1987) designed an experiment to assess the relative importance of familiarity and kinship in young peer-housed pig-tailed macaques' social preferences. They created four categories of test stimuli (familiar kin, unfamiliar kin, familiar non-kin and unfamiliar non-kin) and presented pairs of test stimuli to their subjects. Subjects showed strong preferences for familiar kin over unfamiliar kin and for familiar non-kin over unfamiliar non-kin, but the effects of kinship on their social preferences were more equivocal. When subjects were presented with unfamiliar kin and unfamiliar non-kin, they tended to prefer kin. On the other hand, the monkeys did not distinguish between familiar kin and familiar non-kin.

Based on these two studies, Frederickson & Sackett concluded that '...familiarity alone is responsible for preference in these laboratory choice tests'. They suggested that the findings reported by Wu *et al.* were the product of a type I statistical error. Two additional laboratory studies, which attempted to disentangle familiarity and genetic kinship, failed to demonstrate paternal kin recognition (Welker *et al.* 1987; Erhart *et al.* 1997), whereas a third study provided some evidence of preferences for unfamiliar paternal kin (MacKenzie *et al.* 1985). These findings led most researchers to conclude that phenotypic cues do not play an important role in primate kin recognition systems (e.g. Rendall 2004).

Holmes (2004), one of the authors of the original paper, has questioned Frederickson & Sackett's rationale for discounting the original results. He points out that the two studies generated quite similar patterns for the one comparison that was common to both studies: unfamiliar kin versus unfamiliar non-kin. In both cases, monkeys showed a preference for unfamiliar kin over unfamiliar non-kin, although the authors reached different conclusions about the statistical significance of the results. However, if monkeys can reliably discriminate between unfamiliar kin and non-kin, then why did not they differentiate between familiar kin and familiar non-kin in Frederickson & Sackett's study? It is possible that close, continuous association very early in life is a cue used to discriminate maternal kin from others. If so, infants who are reared from birth in small peer groups may (falsely) label all members of their groups as maternal kin. But when confronted with unfamiliar monkeys, they may make use of a different set of cues, such as similarity to themselves.

The debate about the importance of phenotypic cues in primate kin recognition systems was rekindled when Parr & de Waal (1999) reported that chimpanzee females were able to match digitized photographs of unfamiliar females with their sons (but not with their daughters). Because the chimpanzees were unfamiliar with the individuals in the photographs and had no physical, auditory or olfactory contact with them, their ability to identify mother–son pairs suggested that chimpanzees use visual cues to assess similarity. However, a detailed analysis of features of the images revealed that there were subtle differences in the ways that the photographic images were framed, and this is probably what enabled subjects to match mothers with sons, but not with daughters (Vokey *et al.* 2004).

Several studies indicated that primates can discriminate between paternal kin and others in more naturalistic settings (reviewed by Widdig 2007; discussed subsequently). Although the mechanisms underlying paternal kin recognition in these cases have not been established, some evidence suggests that monkeys do not rely entirely on contextual cues, such as age similarity or maternal associations, to identify paternal kin (Alberts 1999; Widdig *et al.* 2001). For example, Widdig and her co-workers found that rhesus macaques distinguished peers who were paternal half siblings and peers who were unrelated to themselves, suggesting that age proximity is not the only cue that the monkeys used to identify paternal kin.

3. EPOTISTIC BIASES IN PRIMATE SOCIETIES
(a) *Non-gregarious primates*
In a number of prosimian primates, adults spend much of their time alone or in the company of their dependent offspring. In some of these species, maternal kinship structures the neighbourhoods in which females live. Dwarf lemurs (*Mirza coquereli*) in Madagascar forage alone during the night, and rest

alone during the day. However, females tend to establish territories near their mothers, creating a multi-generational matrilineal community of females (Kappeler *et al.* 2002). Similar patterns may characterize some galago species (Nash 2004) as well as orangutans (*Pongo pygmaeus*), the only solitary ape (Delgado & van Schaik 2000).

Grey mouse lemurs, *Microcebus murinus*, elaborate on this pattern. The home ranges of matrilineal female kin are clustered in space, and females forage alone at night. However, females often gather together to sleep during the day and sometimes nurse one another's young (Eberle & Kappeler 2006). These sleeping groups are primarily composed of matrilineal female kin (Radespiel *et al.* 2001; Wimmer *et al.* 2002; Eberle & Kappeler 2006).

(b) *Cooperatively breeding species*
Marmosets and tamarins, members of the subfamily Callitrichinae, live in small territorial groups that are composed of a single breeding pair, several non-breeding adults, who are generally same-sexed siblings of the breeding pair or mature offspring from previous litters of the breeding pair, and dependent offspring (French 1997; Tardiff 1997; Dietz 2004). Breeding females typically give birth to fraternal twins and can produce two litters per year. The cost of reproduction in callitrichids, measured in terms of litter weight and standardized for allometry, is considerably higher than in solitary, pair-bonded or plural breeding primate species (Harvey *et al.* 1986). After females give birth, all mature group members provide extensive help carrying and provisioning infants. Pairs with helpers sustain higher rates of fertility than pairs without helpers.

Genetic chimerism may have facilitated the evolution of cooperative breeding within this lineage. Callitrichid twins typically share a common placenta and chorion (the membrane that surrounds the growing embryo in the uterus). Stem cells are passed from one twin to the other (Haig 1999). This process extends to somatic tissues and gametes (Ross *et al.* 2007). This means that individuals sometimes pass along their twin's genes, not their own. Chimerism effectively raises the degree of relatedness among twins and may increase the inclusive fitness benefits derived from helping to rear nephews and nieces (Haig 1999).

(c) *Species with female philopatry*
There are pronounced matrilineal biases in behaviour in a number of primate taxa that are characterized by female philopatry and male dispersal, particularly cercopithecine primates, including all species of macaques (*Macaca* spp.), savannah baboons (*Papio cynocephalus* spp.) and vervet monkeys (*Clorocebus aethiops*). In these species, affiliative and cooperative behaviours are biased in favour of kin. For example, female baboons spend much of their time in close proximity to related females, and they groom kin at considerably higher rates than they groom unrelated individuals. Similarly, females reconcile conflicts with kin at higher rates than they reconcile conflicts with

non-kin. Females in these species also intervene on behalf of close kin when they are involved in aggressive interactions more often than they intervene on behalf of more distantly related relatives or non-relatives. The most risky forms of intervention tend to be limited to close relatives. For detailed reviews of the kin biases in cercopithecine primate groups, see Berman (2004), Chapais (2001), Kapsalis (2004) and Silk (2001, 2005).

Preferential treatment generally extends to mothers, offspring, siblings, grandmothers, grandoffspring and sometimes to aunts and nieces, but not to more distant kin (Kapsalis & Berman 1996). Thus, the threshold for nepotism seems to be somewhere between 0.25 and 0.125. It is not clear if this threshold represents the boundaries of kin recognition or reflects the fact that it is progressively more difficult to satisfy Hamilton's rule as relatedness declines. Sherman (1980, 1981) suggested that kin selection will not favour the ability to recognize categories of relatives that are not encountered on a regular basis. In the pro-visioned groups of macaques that were first studied in Japan and on Cayo Santiago, predators are rare, food is plentiful, female fertility is high and infant mortality is low. This produces very large matrilineal units and considerable generational overlap. In more naturalistic settings, matrilines are considerably smaller, and certain categories of kin are surprisingly uncommon. For example, adult female baboons virtually never live in groups with adult granddaughters and have very few cousins (Silk *et al.* 2006a).

Maternal kin biases contribute to the formation of matrilineal dominance hierarchies in macaques, baboons and vervets. Mothers sometimes support their juvenile offspring when they are involved in disputes with group members that the mother outranks. As they mature, young females typically acquire rank positions immediately below their mothers (reviewed by Chapais 2002). Mothers typically support younger daughters over older daughters and maturing females normally rise in rank over their older sisters.

Several lines of evidence suggest that nepotistic support plays a critical role in rank acquisition. First, if females are orphaned when they are young, they may not achieve their mothers' original rank (Walters 1980; Johnson 1987). Second, small juveniles from high-ranking matrilines can defeat larger juveniles from lower ranking matrilines when their mothers are nearby, but not when their mothers are some distance away (Datta 1983a,b,c; Horrocks & Hunte 1983). Third, Chapais designed a series of experiments to assess the importance of nepotistic support in the formation of matrilineal dominance hierarchies in macaque groups (Chapais 1988a,b; Chapais *et al.* 1997). The basic protocol involved removing pairs or trios of monkeys from their social group and housing them in temporary subgroups. Chapais (1988a) found that when juveniles were paired with a higher ranking juvenile of their own size and age, they did not challenge them. But when the same juveniles were joined in these subgroups by their mothers ($r = 0.5$), older sisters ($r = 0.25$) or grandmothers ($r = 0.25$), they challenged higher ranking peers,

were frequently supported by their older relatives and successfully reversed their ranks.

Matrilineal dominance hierarchies are remarkably stable over time (Kapsalis 2004), and this was originally attributed to coalitionary alliances among maternal kin (e.g. Chapais 1988*a*,*b*; Silk 2001). However, there is now some uncertainty about the role of nepotistic support in the maintenance of dominance relationships within groups. In an experimental study, Chapais & St-Pierre (1997) showed that alliances among unrelated females against lower ranking females may contribute to the stability of dominance relationships within macaque groups. Moreover, in a series of papers (Henzi & Barett 1999; Barrett & Henzi 2002, 2005), it has been pointed out that the rates of intervention in baboon groups with very stable dominance hierarchies are often quite low and, in some cases, are not seen at all. In some groups, females maintain high ranks for many years, even though they have no adult relatives in the group. Thus, high levels of active coalitionary support from kin may not be needed for females to maintain their ranks.

However, it is possible that the frequency of coalitionary support is not an accurate measure of its importance. The presence of potential allies may deter challenges from subordinate females (Cords 2002). Moreover, less-active forms of coalitionary support may play an important role in mediating disputes among females. Most studies of coalitionary support focus on active forms of intervention, such as chasing or threatening a common opponent. Wittig *et al.* (2007) showed that females sometimes give aggressive vocalizations when they observe conflicts involving others. These 'vocal alliances' occur 1.4 times as often as more active forms of support, and both vocal alliances and active support are biased in favour of close kin (mothers, daughters and sisters). Playback experiments showed that aggressive vocalizations by close relatives of their former opponents altered aggressors' behaviour: they were more likely to behave submissively and less likely to approach their former opponents.

Kin biases in behaviour are linked to female reproductive success in two different ways. First, high-ranking cercopithecine females tend to mature at earlier ages, grow faster, produce healthier infants, have shorter interbirth intervals and achieve higher lifetime fitness than low-ranking females (reviewed by Harcourt 1987; Silk 1993; Altmann & Alberts 2003; Cheney *et al.* 2004). The magnitude of the effects of dominance rank varies over time and across populations. However, any reproductive advantages that high-ranking females accrue will be magnified over time because dominance hierarchies remain stable over time. Second, female baboons, who are more fully integrated into their social groups (Silk *et al.* 2003) and have stronger social bonds with adult females (Silk *et al.* 2009), have high survivorship among their offspring than other females within their groups. These effects are independent of differences in female dominance rank and variation in the quality of the environment in which females live.

We know much more about the behaviour of macaques, baboons and vervets than we do about the behaviour of other primates with female philopatry, such as South American capuchin monkeys (*Cebus* spp.) and ring-tailed lemurs (*Lemur catta*). The most complete analyses of maternal kin biases among capuchins come from a 10-year study of one group of white-faced capuchins, *Cebus capucinus*, in Costa Rica (Perry *et al.* 2008). In this group, females selectively groomed and associated with their mothers, daughters and maternal sisters (both full and half sisters). Maternal kin biases were more pronounced when the group was relatively large and average degrees of relatedness among females were relatively low than when the group was smaller and average degrees of relatedness among females were relatively high. Although females showed kin biases in support, they did not form matrilineal dominance hierarchies and the dominance hierarchy was not as stable as those in cercopithecine species.

Ring-tailed lemur groups are composed of several matrilines. Like white-faced capuchins, female ring-tailed lemurs show nepotistic biases in affiliative behaviour, but do not form matrilineal dominance hierarchies (Nakamichi 1997; Nakamichi & Koyama 1997; Jolly & Pride 1999; Sauther *et al.* 1999). Although coalitionary aggression is rare (Nakamichi & Koyama 1997; Sauther *et al.* 1999), nepotistic alliances may play an important role in some circumstances. For example, Nakamichi (1997) describes one case in which a female was able to regain her high-ranking position with the support of her adult daughter. Moreover, when groups become too large, members of one matriline may collectively target members of another matriline for eviction (Sauther *et al.* 1999). Although single females never move from one group to another, mothers and daughters are sometimes able to do so together (Sauther *et al.* 1999).

Several recent studies have demonstrated patrilineal kin biases in species with female philopatry. In baboon and rhesus macaque groups, females are more likely to associate with and groom paternal half sisters than unrelated females (Widdig *et al.* 2001, 2002; Smith *et al.* 2003; Silk *et al.* 2006*a*). Female rhesus macaques do not selectively support their paternal half sisters in agonistic encounters, but they do avoid intervening against them (Widdig *et al.* 2006). Juvenile mandrills show preferences for adult paternal half siblings over unrelated adults, but not for juvenile paternal half siblings over unrelated juveniles (Charpentier *et al.* 2007). Females baboons and macaques generally form substantially stronger bonds with maternal half sisters than with paternal half sisters (Widdig *et al.* 2001, 2002; Silk *et al.* 2006*a*), but female baboons form stronger bonds with their paternal half sisters when close maternal kin are not available (Silk *et al.* 2006*a*). In contrast to the patterns observed in baboon and macaque groups, white-faced capuchins do not show preferences for paternal half sisters over unrelated individuals (Perry *et al.* 2008), even though male reproductive skew is as high in these groups as it is in baboon and macaque groups (Muniz *et al.* 2005). There are not yet enough studies of paternal kin discrimination to identify ecological, demographic or phylogenetic factors that might facilitate paternal

kin discrimination or favour paternal kin biases in behaviour in some species, but not others.

(d) *Species with male philopatry*

Male philopatry characterizes a small number of primate species, including chimpanzees, bonobos (*Pan paniscus*), spider monkeys, muriquis and woolly spider monkeys (Pusey & Packer 1987). Social relationships among male chimpanzees have been studied almost as extensively as social relationships among cercopithecine primate females. Chimpanzee males spend a considerable amount of time in parties with other males, and males groom, hunt, share meat, aid and patrol the borders of their territories with one another (Muller & Mitani 2005; Gilby & Wrangham 2008). The structure of males' social bonds is strikingly similar to that of social bonds among female baboons, although the extent of nepotism is considerably less pronounced (Mitani 2009). In chimpanzee communities, males tend to form close relationships with their maternal brothers when they are available (Nishida 1979; Goodall 1986; Langergraber *et al.* 2007; Mitani 2009), but many males do not have brothers in their groups and kinship does not seem to be a necessary ingredient of close relationships among male chimpanzees (Langergraber *et al.* 2007; Gilby & Wrangham 2008). Male chimpanzees do not seem to discriminate between paternal half brothers and unrelated males (Langergraber *et al.* 2007). For male chimpanzees, contingent reciprocity may play a more important role than kinship in shaping social relationships.

Although chimpanzee males spend much of their time in the company of other males, they do spend some time travelling and foraging alone. When males are alone, they range in the core areas of their mothers, even if their mothers are no longer alive (Murray *et al.* 2008). High-ranking females occupy higher quality core areas than low-ranking females, so their sons may gain advantages from inheriting their core areas.

There are a number of parallels between male chimpanzees, spider monkeys and male muriquis, although our knowledge of the social dynamics in these New World monkeys is much less complete. Like chimpanzees, male spider monkeys and muriquis associate and affiliate at high rates (Strier *et al.* 2002; Slater *et al.* 2009). Spider monkeys launch joint raids into neighbouring territories (Aureli *et al.* 2006), and male muriquis cooperate in hostile intergroup encounters (Strier 1994). Muriqui males maintain egalitarian social relationships and share access to receptive females (Strier *et al.* 2002). Limited evidence suggests that maternal kinship is not a necessary ingredient of social bonds among male muriquis (Strier *et al.* 2002), but we do not yet know whether there are kin biases among spider monkeys.

(e) *Kin biases in the dispersing sex*

Maternal kin biases can also be detected in some species in which females emigrate from their natal groups. For example, most female mountain gorillas (*Gorilla gorilla berengei*) leave their natal groups, but dispersing females sometimes join groups that contain females from their natal group. In some cases, females, who are likely to be sisters, emigrate together (Harcourt & Stewart 1987). Thus, even though females are not philopatric, nearly 70 per cent of the females spend at least some of their reproductive years in the company of female kin (Watts 1996). When females live with related females, they tend to show strong nepotistic preferences. Adult female mountain gorillas spend more time resting and feeding near their relatives than non-relatives, rarely fight with kin and are more likely to groom and support kin than non-kin (Harcourt & Stewart 2007). Similarly, some chimpanzee females remain in their natal groups throughout their lives. When they do, they often develop enduring social relationships with their mothers (Williams *et al.* 2002; Gilby & Wrangham 2008). In red howler (*Alouatta seniculus*) groups, opportunities for maternal kin biases vary over the course of time. New groups are formed when solitary migrating females meet, form ties, attract males, establish territories and begin to reproduce (Pope 2000). As time passes, the natal females are recruited and the average degree of relatedness among females rises. Eventually, the average degree of relatedness approaches 0.5 (Pope 1998, 2000). This has adaptive consequences for females because their reproductive success is correlated with the degree of relatedness within their groups (Pope 2000).

(f) *Paternal care*

Until recently, true paternal care was assumed to be limited to pair-bonded species with high paternity certainty. However, a growing body of evidence suggests that paternal care is more widespread. In some multi-male baboon groups, males selectively support their own offspring in agonistic encounters (Buchan *et al.* 2003) but in others paternal biases are not detected (Moscovice *et al.* 2009). The presence of fathers also accelerates the maturation of their offspring (Charpentier *et al.* 2008). Male chimpanzees play more with their own offspring than with unrelated infants (Lehmann *et al.* 2006), and juvenile mandrills associate at higher rates with their fathers than with unrelated males (Charpentier *et al.* 2007). Males in a number of species protect their own offspring from harassment by potentially infanticidal males (Palombit 2000).

Alliances among fathers and sons may develop in some primate species. When local habitats are saturated and red howler groups are large, single males have difficulty defending groups of females. In these situations, red howler males sometimes form coalitions. Although the dominant male within the coalition monopolizes conceptions, males collectively defend females against incursions by foreign males and jointly challenge residents for access to groups of females. Some coalitions are composed of related males, often fathers and sons (Sekulic 1983). Father–son coalitions stay together considerably longer and have more stable dominance relationships than coalitions of unrelated males (Pope 1990). Kinship may enhance the stability of coalitions

because the lower-ranking male gains inclusive fitness benefits by assisting his father or son to reproduce.

Similarly, mountain gorillas generally form one-male groups, but multi-male groups can be formed when silverbacks are joined by younger natal males (Harcourt & Stewart 1997; Watts 2000). Male residents cooperate in aggression against outside males. The males who form these coalitions may be fathers and sons (Watts 2000). When lowland gorilla (*Gorilla gorilla gorilla*) males leave their natal groups, they sometimes establish territories within the same area. The resident males in neighbouring lowland gorilla groups are closely related (Bradley *et al*. 2004), and their relatedness may explain why male silverbacks from neighbouring territories have relatively peaceful relationships.

Patrilineal associations are also suspected to occur in hamadryas baboons (*Papio hamadryas*), which form multi-level societies (Stammbach 1987). The resident males in one-male units are sometimes replaced by males who are thought to be their sons (Sigg *et al*. 1982). Although one-male units spend much of their time near one another, leaders of one-male units rarely attempt to take females from other males in their clans and are quite tolerant of the males in their clans. Based on phenotypic similarities, males in the same band are thought to be related (Stammbach 1987).

4. DO PRIMATES CONFORM TO HAMILTON'S RULE?

There is abundant evidence of nepotistic biases in primate groups. Altruistic behaviours, including grooming, coalitionary support and food sharing, are selectively directed towards genetic relatives. Moreover, these behaviours are preferentially directed towards closer kin over more distant kin. Both these patterns are consistent with qualitative predictions derived from kin selection theory and are commonly interpreted as the product of kin selection.

It is much more difficult to determine whether the distribution of altruistic behaviour fits quantitative predictions derived from Hamilton's rule, $br > c$. This is because we are unable to measure the fitness benefits of altruistic acts for recipients and the costs of altruistic acts for donors. There is not even complete agreement about whether particular forms of behaviour are altruistic (Chapais 2001; Chapais & Bélisle 2004). For example, Dunbar (1988) and Dunbar & Sharman (1984) concluded that grooming must not be costly to perform because females do not reduce the amount of time that they devote to social grooming when they are under time budget constraints and do reduce the amount of time that they devote to other energetically expensive activities. But the same data could be interpreted to mean that grooming is costly, but serves essential social functions, and is too important to be neglected even in difficult times. Similarly, there is debate about the costs and benefits of coalitionary aggression, sharing access to food, giving alarm calls, forming friendships with new mothers and so on.

Quantitative predictions about the distribution of altruism are difficult to formulate because they depend on assumptions about the shape of the curve of benefits across time. For example, if the benefits of being groomed are constant across time, then all grooming should be directed towards the closest kin available (Altmann 1979). But if there are declining returns from grooming across time, then groomers should eventually switch to less closely related partners. Constraints on time and energy, variation in the availability of preferred categories of partners, the opportunity costs of choosing more closely related partners over more competent partners, the possible benefits derived from reciprocity and a number of other factors further complicate predictions about the deployment of altruism in primate groups (Chapais & Bélisle 2004). As a result, 'the optimal allocation of altruism is unknown' (Altmann 1979), and Hamilton's rule cannot be tested with any degree of precision.

Chapais has suggested that this ambiguity may have encouraged us to overestimate the role of kin selection and underestimate the importance of other forces in the distribution of altruistic behaviour (Chapais 2001, 2006; Chapais & Bélisle 2004). There are at least two processes besides kin selection that could generate high rates of interaction among kin: (i) kin biases could reflect an attraction to animals of similar rank or (ii) kin biases could be a by-product of extended associations between mothers and their offspring.

In species with matrilineal dominance hierarchies, nepotistic biases may reflect an attraction to animals of similar rank, not an attraction to kin *per se*. This argument was first proposed by Seyfarth (1977), who suggested that females might exchange grooming for support in agonistic conflicts. Because high-ranking females make the most powerful allies, he predicted that all females would direct their grooming efforts towards the highest ranking females in their groups. However, time budgets constrain the amount of time available for being groomed (Dunbar 1991), so females would have to compete for access to the highest ranking females. High-ranking females would be able to monopolize access to other high-ranking females, forcing lower ranking females to settle for grooming partners closer to their own rank and to trade grooming in kind. Related females occupy adjacent ranks, so this process would incidentally generate high rates of grooming among kin. Thus, kin biases emerge from competition over access to high-ranking allies. Several of the primary predictions of Seyfarth's model are well supported. Correlations between grooming and support are consistently observed, and monkeys interact at high rates with those of similar rank (Schino 2001; Schino & Aureli 2007).

However, there are several reasons to suspect that kin biases in behaviour are not simply an artefact of an attraction to females of similar rank. First, in baboons and macaques, females' preferences for maternal kin are stronger than their preference for unrelated females of adjacent rank (Silk 1982; De Waal 1991; Kapsalis & Berman 1996; Silk *et al*. 1999). Second, dominance rank and maternal kinship

are disassociated in some species, but nepotistic biases persist (hanuman langurs, Borries *et al.* 1992; mountain gorillas, Watts & Pusey 1993; capuchins, Perry *et al.* 2008; ring-tailed lemurs, Sauther *et al.* 1999). Third, female baboons and macaques show preferences for paternal kin, who do not hold adjacent ranks (references above).

In species with female philopatry, matrilineal biases in behaviour may be the by-product of mother–infant association patterns, not the products of kin selection (Chapais 2001, 2006). Mothers form close and enduring ties with their offspring. This means that as mothers wean one infant and produce another, they continue to associate with their older offspring. Maternal siblings are drawn together by their joint association with their mother. As daughters mature and produce offspring of their own, grandmothers and their grandoffspring will be brought together often. Aunts are similarly connected to their sister's daughters, their own nieces. If females interacted at random with their associates, high rates of interaction among kin would emerge without any deliberate preference for interacting with relatives.

This sort of process may influence the interactions of females in some situations. Young macaques interact at higher rates with the offspring of females that their mothers associate with at higher rates, and the degree of infants' kin biases is linked to the degree of their mothers' kin biases (Berman 2004). In the Amboseli baboon groups, females groom and associate with their adult sisters and their sisters' daughters (nieces) at higher rates than they associate with unrelated females. Rates of interactions between aunts and nieces decline when the female who connects them dies (the aunt's sister and the niece's mother; Silk *et al.* 2006*a*). But there are several reasons to believe that this is not the whole story. In the Amboseli baboon population, rates of interaction among maternal and paternal sisters rise after their mothers' deaths. This suggests that relationships among sisters are the product of a positive attraction towards preferred categories of partners. Moreover, if high rates of affiliation among close kin are simply a by-product of high rates of association, then we would also expect to observe elevated rates of aggression among them (Perry *et al.* 2008). But rates of aggression among capuchins do not track rates of affiliation or the degree of relatedness among females, suggesting that 'kin-biased distribution of grooming and coalitionary support is a product of selection for specifically benign dispositions towards females recognized as close kin' (Perry *et al.* 2008).

Chapais also points out that cooperative interactions among related females may be regulated by contingent reciprocity and mutualism, rather than kin selection. In fact, there is good reason to believe that these processes will reinforce each other. Kinship can enhance the stability of contingent reciprocity by making defections less costly and would also increase the benefits derived from mutualistic partnerships. There is some evidence that kinship enhances contingent reciprocity in baboon groups as females form more well-balanced grooming relationships with close female kin than with more distantly related kin and

unrelated partners (Silk *et al.* 2006*a*,*b*; see also Janus 1989). Similarly, high-ranking matrilines show the most pronounced nepotistic biases (Berman 1980; Silk *et al.* 1999), perhaps because kin selection enhances the individual benefits derived from developing alliances with powerful partners.

At the same time, reciprocity and mutualism do not provide plausible explanations for some forms of unilateral costly kin-biased behaviour described earlier. These include rank reversals among aged female baboons and their daughters, support for immature macaques involved in disputes with individuals from higher ranking families, fathers' protection of offspring from infanticidal attacks and female macaques' tolerance of subordinate relatives at feeding sites.

5. SUMMARY AND CONCLUSIONS

More than 100 years after Darwin met Jenny in the London zoo, the first detailed descriptions of the social organization and behaviour in primate groups were published. Over the last 50 years, these accounts have been amplified and extended, as primatologists have documented the frequency, distribution and function of social interactions in a diverse range of primate species. Across the primate order, kinship plays an important role in structuring the evolution of primate social systems and the development of social relationships in primate groups. There are pronounced nepotistic biases in the distribution of altruistic behaviours such as grooming, coalitionary support and food sharing, and these biases emerge whenever relatives live together for extended periods of time. The distribution of cooperative behaviours conforms to qualitative predictions derived from Hamilton's rule, but uncertainties about costs and benefits of behavioural acts make it impossible to test predictions derived from Hamilton's rule with precision. It seems likely that other processes, including contingent reciprocity and mutualism, may complement the effects of kin selection and amplify the extent of nepotistic biases in behaviour.

There are important gaps in our knowledge of nepotism in primate groups. First, we still know much more about kin biases in behaviour in cercopithecine primate species and chimpanzees than we do about kin biases in prosimians, New World monkeys, colobines or the other great apes. This makes it difficult to draw inferences about the forces that have shaped the evolution of sociality within the primate order. Second, most behavioural analyses focus on the pattern of interactions among maternal kin, but it is becoming clear that nepotism may extend to paternal kin in some species. Species with high reproductive skew and well-defined birth cohorts are likely candidates for patrilineal biases in behaviour. Third, it may be fruitful to explore the mechanisms underlying kin recognition in primates. Reassessment of experimental findings and new data from field studies suggest that familiarity, age similarity, mating history and phenotypic features may all contribute to kin recognition. Fourth, mutualism and reciprocity often complement the effects of kin selection. Carefully

controlled experimental studies can be used to tease apart these processes in the laboratory but in nature they may often be confounded, making it difficult to weigh their contributions to the evolution of cooperation in primate groups.

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