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The adaptive value of sociality in mammalian groups

Joan B. Silk*

Department of Anthropology, University of California, Los Angeles, CA 90095, USA

According to behavioural ecology theory, sociality evolves when the net benefits of close association with conspecifics exceed the costs. The nature and relative magnitude of the benefits and costs of sociality are expected to vary across species and habitats. When sociality is favoured, animals may form groups that range from small pair-bonded units to huge aggregations. The size and composition of social groups have diverse effects on morphology and behaviour, ranging from the extent of sexual dimorphism to brain size, and the structure of social relationships. This general argument implies that sociality has fitness consequences for individuals. However, for most mammalian species, especially long-lived animals like primates, there are sizable gaps in the chain of evidence that links sociality and social bonds to fitness outcomes. These gaps reflect the difficulty of quantifying the cumulative effects of behavioural interactions on fitness and the lack of information about the nature of social relationships among individuals in most taxa. Here, I review what is known about the reproductive consequences of sociality for mammals.

Keywords: sociality; fitness; reproductive success; social organization; social bonds; reproductive strategies

1. INTRODUCTION

> Although many studies of insects, birds, and mammals have documented the functional significance of single interactions such as fights, the reproductive benefits of long-term social bonds are less immediately obvious.
> (Cheney *et al.* 1986)

It has been 20 years since this observation was made. During the interim, we have documented some of the characteristics that contribute to individual variation in reproductive performance. For example, in ungulates, female reproductive success is influenced by their age, maternal experience and longevity (Clutton-Brock *et al.* 1988; Gaillard *et al.* 2000; Weladji *et al.* 2006). For animals that live in social groups, reproductive success is also influenced by the outcome of certain types of social interactions. Thus, there are positive correlations between dominance rank and reproductive performance in many taxa (Pusey & Packer 1997). In some species, social conditions influence the physiological responses of individuals. For example, the presence of familiar conspecifics buffers the effects of experimentally-induced stress in rats, mice, goats and monkeys (House *et al.* 1988; Seeman & McEwen 1996). Social integration is linked to reduced levels of basal cortisol levels in male baboons (Sapolsky *et al.* 1997), and the existence of close bonds between adult male baboons and lactating females mitigates females' stress responses in the presence of potentially infanticidal males (Beehner *et al.* 2005; Engh *et al.* 2006*a*). Although it seems plausible that the quality and stability of social bonds may have long-term reproductive consequences for individuals, the links between sociality, social relationships and fitness remain quite tenuous.

This represents a critical gap in our knowledge because we have built a body of theory about the functional consequences of sociality. The forms of social cognition that are described in this volume have presumably been favoured by natural selection because they enhance the ability of group-living individuals to reproduce successfully. These capacities are deployed as animals develop relationships, form alliances, court mates and compete for resources with conspecifics. The capacity to form and maintain social bonds plays an integral role in functional interpretations of many aspects of behaviour, such as reconciliation in monkeys (Aureli & de Waal 2000), coalitions in cetaceans (Connor *et al.* 1998; Connor 2007) and pair bonding in microtine rodents (Young & Wang 2004). To critically evaluate these hypotheses, we must be able to document the reproductive consequences of sociality for individuals.

According to behavioural ecology theory, sociality evolves when the net benefits of close association with conspecifics exceed the costs (Krause & Ruxton 2002). In mammals, sociality can be beneficial for individuals because it provides greater protection from predators, enhances success in locating or maintaining access to resources, creates mating opportunities or reduces vulnerability to infanticide. At the same time, sociality can be costly for individuals because it increases competition over access to resources and mating opportunities, exposes them to infection and may increase their conspicuousness to predators. The nature and relative magnitude of the benefits and costs of sociality are expected to vary across species and

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*jsilk@anthro.ucla.edu

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habitats. For primates and many other mammals, it is generally thought that the main benefit of sociality is protection against predators and the main cost of sociality is increased competition for resources with other group members (e.g. Sterck *et al.* 1997; Isbell & Young 2002).

When sociality is favoured, animals may form groups that range from small pair-bonded units to huge aggregations. The size and composition of social groups have diverse effects on morphology and behaviour, ranging from the extent of sexual dimorphism (primates: Clutton-Brock *et al.* 1977; Plavcan 2003; ungulates: Clutton-Brock *et al.* 1980; Pérez-Barbería *et al.* 2002) to relative brain size (primates: Sawaguchi & Kudo 1990; Dunbar 1992, 1995; Barton & Dunbar 1997; cetaceans: Connor *et al.* 1998; carnivores and insectivores: Dunbar & Bever 1998; ungulates: Shultz & Dunbar 2006), and the prevalence of infanticide (Hausfater & Hrdy 1984; van Schaik & Janson 2000).

This general argument implies that sociality has fitness consequences for individuals. However, for most mammalian species, especially long-lived animals like primates, there are sizable gaps in the chain of evidence that links sociality and social bonds to fitness outcomes. These gaps reflect the difficulty of quantifying the cumulative effects of behavioural interactions on fitness. This problem is common to almost all studies of the adaptive function of social behaviour in animals. Instead, we generally rely on what Grafen (1991) called the 'phenotypic gambit', the assumption that the short-term benefits that individuals derive from social interactions are ultimately translated into long-term differences in fitness. For example, if group size reduces vigilance time, then individuals will be able to forage more efficiently, and enhanced foraging efficiency will be ultimately transformed into fitness gains. Similarly, we assume that animals which are regularly supported in agonistic confrontations or groomed frequently gain short-term benefits that enhance their lifetime fitness. Social relationships that provide these kinds of short-term benefits are therefore assumed to have selective value for individuals. This logic is sometimes extended one step further. It is hypothesized that the magnitude of the investment that animals make in their social relationships provides a measure of their adaptive value (Kummer 1978). This hypothesis cannot be tested without information about the adaptive consequences of social bonds.

The goal of this paper is to venture beyond the phenotypic gambit and to review what we know about the adaptive consequences of sociality in mammalian groups. I focus on females for both theoretical and practical reasons. Males disperse more regularly and over longer distances than females do in most mammalian taxa (Greenwood 1980; Waser & Jones 1983), including primates (Pusey & Packer 1986). Female philopatry enhances the potential for cooperative relationships to arise through kin selection, and may thus facilitate the development of social bonds and the formation of social groups. Practical considerations also favour an emphasis on females because it is considerably easier to assess female reproductive performance than male reproductive performance in most species.

If living in social groups confers fitness benefits on females, then it should be possible to demonstrate that *intraspecific* variation in sociality influences female reproductive success. Group size is the dimension of sociality that is most commonly evaluated in this context, partly because it is straightforward to measure. However, groups can also differ in various aspects of their composition, such as the ratio of adult males to females, the age structure or the degree of relatedness among group members. Variations in any or all of these aspects of group composition might influence the reproductive performance of individuals. Finally, there may be fitness consequences associated with variation in the number, quality and stability of social bonds that females form.

Here, I review published information about the effects of intraspecific variation in group size, group composition and the nature of social bonds on the reproductive performance of females in mammalian species. Although much of the work on social cognition has focused on primates, I have expanded the taxonomic scope of this review beyond primates for several reasons. First, there is no particular reason to think that the evolutionary consequences of sociality in primate females are different from the evolutionary consequences of sociality in other mammalian taxa. Primate females share basic features of their reproductive biology with females in other mammalian taxa, and face many of the same tradeoffs between the costs and the benefits of living in social groups. Second, some valuable information about the proximate and ultimate consequences of sociality come from experimental studies that would be impractical to conduct on primates. Third, there is a vast literature on mammals which provides a rich source of evidence about the adaptive consequences of variation in sociality.

2. EFFECTS OF GROUP SIZE

The size of animal groups reflects the combined effects of the benefits and costs of grouping. For any particular species in any particular habitat, there will be some group size which maximizes the fitness of individuals. This means that females which live in groups that are smaller or larger than the optimal size will reproduce less successfully than females living in intermediate-sized groups. Considerable theoretical and empirical research on optimum group size indicates that the size of groups that animals actually live in often exceeds the optimal group size. The discrepancy between the optimal and the actual size of groups is related to mechanisms that regulate group size. Animals living in groups that are larger than the optimal group might try to oust other residents or disperse themselves. They might also attempt to exclude immigrants. All of these courses of action will be costly to individuals who undertake them. Moreover, animals that make efforts to regulate group size provide benefits to other group members, thus providing a form of altruistic public service. As a result, animals will often find themselves living in groups that exceed the optimal size.

If the individual costs of regulating group size tend to lead groups to exceed the optimal size, then we might expect to find negative relationships between group size and female reproductive performance under some circumstances. For example, according to the ecological constraints model (Chapman & Chapman 2000), an increase in group size produces an increase in the distance that members of groups must travel each day because larger groups deplete food patches more rapidly or require larger search fields. Animals that travel further expend more energy and reproduce less efficiently. Day range and group size are positively associated in a variety of primate and carnivore species (Wrangham *et al*. 1993). These kinds of ecological pressures may have broad impacts in mammalian species. Clutton-Brock and his colleagues (2001) have observed that: 'In social mammals whose young are reared principally by their parents and are rarely (or never) fed directly by other group members, competition for resources commonly increases in large groups and breeding success either declines with increasing group size or shows no consistent relation to it'.

Competition for resources may not be the only factor producing a negative relationship between group size and female reproductive performance. For example, in some species, such as langurs and lions, large groups of females are attractive targets for takeover attempts by males. If male takeovers are associated with infanticide, as is the case in a number of mammalian species (van Schaik & Janson 2000), then rates of infant mortality may be higher in large groups than in small ones.

There may also be circumstances in which positive correlations between group size and reproductive performance are expected to occur. For example, Clutton-Brock and his colleagues (2001) noted that '…positive relations between breeding success and group size are common in social mammals whose young are reared by helpers'. Similarly, for species that do not rely on foods which occur in discrete depletable patches, including some folivores, there may be little cost associated with living in large groups (Chapman & Chapman 2000).

Here, I review evidence about the effects of group size on reproductive performance in a range of mammalian taxa. Following the observation of Clutton-Brock *et al.* (2001) that the relationship between group size and female fitness tends to be negative or neutral when females rear their young alone, but positive when young are reared by helpers, species are loosely ordered by the extent of reproductive skew and the amount of assistance that females receive from other group members. At one end of the continuum are plural breeding species in which all females regularly reproduce and parents, particularly mothers, provide nearly all of their own infants' care. At the other end of the continuum are species in which reproduction is monopolized by a single breeding female, and females are unable to reproduce without non-breeding helpers. In the middle are plural breeding species with communal care of offspring. The relationship between group size and female fitness is expected to become increasingly positive as we move across this continuum.

(a) *Plural breeding species without communal care of young*

Long-term studies of yellow-bellied marmots (*Marmota flaviventris*) in Colorado conducted by Armitage and his colleagues provide detailed information about the effects of sociality on female reproductive performance. Yellow-bellied marmots live in montane meadows in western North America, and they typically form groups composed of several breeding females and their offspring (Blumstein & Armitage 1999). Females cooperatively defend their home ranges against intruders (Allainé 2000). They hibernate alone at low altitudes and together at higher elevations (Blumstein & Armitage 1999). Offspring remain in their natal areas through the first year of life. Then, nearly all yearling males disperse, while about half of all yearling females remain in their natal territories. The recruitment of daughters leads to high degrees of relatedness among females within yellow-bellied marmot groups (Allainé 2000). Females reproduce more successfully in groups that contain multiple females than in groups that contain only one female. However, females that live in exceptionally large groups reproduce less successfully than females that live in intermediate-sized groups (Armitage & Schwartz 2000). Very large groups do not occur often and are unlikely to persist from one year to the next. When group size is reduced through natural causes, females' reproductive success improves. Female reproductive success in very large groups is apparently depressed by competition among females.

Further analyses of the same dataset indicate that the effects of group size have the most pronounced effects on young females. Females who begin to reproduce as 2-year-olds have greater individual fitness than females who delay reproduction (Oli & Armitage 2003), but less than half of the females who survive to age 2 begin to reproduce at this age. Two-year-old females are substantially more likely to reproduce if there are no older females in the group, but after females have begun to reproduce the number of females present has no subsequent effect on their reproductive performance. Thus, the number of females that are present in the group when females begin to reproduce has a significant negative effect on their lifetime fitness. Although young females are reproductively suppressed in large groups, they may be even worse off if they attempt to disperse. Dispersing animals suffer high rates of mortality and few suitable territories are available. Moreover, if females do find a vacant territory, they will constitute a matriline of one and are unlikely to reproduce successfully (Armitage & Schwartz 2000).

Tuco-tucos (*Ctenomys sociabilis*) are small subterranean rodents from southwestern Argentina (Lacey 2004). They form groups that contain one adult male, one to six breeding females and their offspring. All females reproduce and rear their young in a single nest in an underground burrow, and all group members participate in burrow maintenance and predator detection. Dispersal is uncommon and is limited to a short period at the end of females' first year. Females who do not disperse at this stage remain in their natal groups throughout their lives. Females who disperse and survive to reproduce, breed alone as yearlings, but may be joined by philopatric daughters in subsequent breeding seasons. There is a strong negative effect of group living on females' reproductive performance. Females living in groups produce fewer surviving offspring per capita than lone females. Moreover, for females that live in groups, there is a negative relationship between the number of adult females and the per capita number of pups reared to weaning. There is evidence that group size has a direct effect on female reproductive performance because decreases in group size from year to year are associated with increases in female reproductive success across years. Even though lone females produce significantly more surviving offspring than group living females, there are no detectable differences in the lifetime reproductive success of dispersing and philopatric females, perhaps because group living females are more likely to survive from one year to the next.

On the island of Rhum, female red deer (*Cervus elaphus*) occupy home ranges of approximately 2 km^2 and make intensive use of smaller core areas within their ranges (Clutton-Brock *et al.* 1982, 1988). Maternal kin share a common home range and females' core areas often overlap or adjoin the core areas of their mothers and sisters. Matrifocal groups range in size from 2 to 12 breeding females. Females that belong to very small and very large matrilines reproduce less successfully than females that live in matrifocal groups of intermediate size. Competition with related females for preferred resources within their core areas seems to reduce the reproductive success of females in large matrifocal groups.

Bottle-nose dolphins (*Tursiop* spp.) live in fission–fusion groups. While males form stable associations with other males and cooperate in mating efforts, females form less stable associations (Connor *et al.* 1998, 2001). Some females are consistently sighted in larger parties than other females, although the range of variation in female party size is relatively small (Mann *et al.* 2000). It is not entirely clear how females might benefit from associating with other females, but calves may be safer from predation when females are in parties. This is consistent with the observation that party size is largest when calves are youngest. However, mean party size is unrelated to female reproductive success, measured as the number of calves raised over a 10-year period.

Comparisons of the lifetime reproductive success of females living in large and small groups of long-tailed macaques (*Macaca fasicularis*) suggest that living in large groups depresses female fitness (van Noodwijk & van Schaik 1999). However, it is not entirely clear why the fitness of females living in large groups is reduced. There may be higher levels of resource competition in large groups. This is supported by the fact that females in large groups spend more time travelling and less time resting than females in smaller groups do (van Schaik *et al.* 1983). Resource competition may influence females' fertility in several different ways. It may limit the amount of food that females obtain and thus impair their nutritional status or increase the amount of harassment they receive and elevate stress levels that females experience. Both of these factors could contribute to differences of the reproductive performance of females in large and small groups.

A recent analysis of cortisol levels in free ranging ring-tailed lemurs (*Lemur catta*) living in groups of different sizes provides evidence that females' stress levels are elevated in groups that deviate from the optimal size (Pride 2005). Lemurs live in groups that range in size from approximately 5 to 25 individuals. Price found that females' cortisol levels were higher in small and large groups than in intermediate-sized groups. Cortisol levels were lowest in groups that were close to the mean group sizes that characterize ring-tailed lemurs in the population.

Comparative analyses conducted on a number of primate taxa suggest that the females which live in large groups suffer reproductive costs. van Schaik (1983) compiled data from a number of primate populations representing about a dozen primate genera. For each population, he evaluated the relationship between the number of females in groups and their fertility, measured as the number of infants per female. The slopes of the regressions were predominantly negative, indicating that females' fertility is depressed in the largest groups. Very similar findings have been obtained for lion-tailed macaques (Kumar 1995) in Tamil Nadu, langurs (Treves & Chapman 1996) and howler monkeys (Treves 2001) using larger datasets and somewhat different analytic methods. These data suggest that females often find themselves living in groups that exceed the optimum group size.

(b) *Plural breeding species with communal care of young*

Prairie voles (*Microtus ochrogaster*) live in extended family groups (Solomon 1991, 1994; Marfori *et al.* 1997; Hayes 2000; McGuire *et al.* 2002; Hayes & Solomon 2004). Prairie vole groups are typically composed of several adults and offspring from previous and current litters (McGuire *et al.* 2002). In some cases, more than one female produces offspring (Hayes & Solomon 2004). However, the majority of male and female offspring remain in their natal groups as non-breeding helpers. Adult males share nests with females and help care for pups (Gruder-Adams & Getz 1985; McGuire & Novak 1984; Oliveras & Novak 1986). All group members help to brood, groom and retrieve pups (Solomon 1991). Prairie vole pups benefit from the presence of non-breeding helpers. Pups that are reared in groups with helpers live longer than pups reared by a single female (Getz *et al.* 1997; McGuire *et al.* 2002). Pups that are reared with helpers also spend less time alone in the nest, develop faster and weigh more at weaning than pups reared by a breeding pair alone (Solomon 1991). These differences in body weight may have important effects on lifetime reproductive success because higher body weight at weaning is associated with higher probabilities of reproducing in the following year, being chosen as a mate by a member of the opposite sex, and winning competitive encounters over mates with members of the same sex (Hayes & Solomon 2004).

Giant gerbils (*Rhombomys opimus*) are desert-adapted rodents which live in groups that consist of one male and one to six related females (Randall *et al.* 2005). They occupy interconnected burrows and cooperatively defend their territories, harvest food and contribute to predator detection. Pups from different litters interact freely after they emerge from their burrows and females with and without pups provide some care for pups. Females are more philopatric than males and the likelihood that females will disperse is linked to local population densities. When population densities are high, dispersal opportunities are limited, hence females tend to remain in their natal territories and group size increases. Group size has no consistent effect on females' reproductive performance. The number of emergent pups per female and pup survivorship do not differ among females who live alone, with just one male, and in larger groups.

Banded mongoose (*Mungos mungo*) live in mixed sex groups that contain multiple adult males, multiple breeding females and their offspring (Cant 2000; de Luca & Ginsberg 2001; Gilchrist *et al.* 2004). Nearly all females become pregnant during each highly synchronized breeding event and then all give birth at the same time in the same den. Pups remain in the den for approximately 30 days, and while they are in the den, all group members help to babysit them. Mothers seem to nurse pups indiscriminately (Cant 2000). As the number of breeding females increases, the per capita number of pups emerging from the den increases (Cant 2000). Litters produced by one or two females routinely fail completely, while litters produced by larger number of females are progressively more likely to survive to emergence.

When the pups emerge, all group members provide care for them (Cant 2000; Gilchrist 2004; Hodge 2005). Most pups form stable associations with a single helper, or 'escort', who provisions and protects them from predators. Most escorts are yearlings. There is considerable variation in the amount of time that pups spend with escorts. Pups that spend more time in association with escorts grow faster and weigh more at independence than pups from the same litter that spend less time with escorts (Hodge 2005). Pups that spend more time with escorts are also more likely to survive to 1 year of age, probably because pups are less vulnerable to predation when they are with escorts (Gilchrist 2004; Hodge 2005). Differences in growth rates are likely to have important effects on lifetime fitness because weight at independence is correlated with weight at 1 year, and females that weigh more at independence conceive their first litters significantly earlier than lighter females (Hodge 2005). Hodge's analyses are particularly powerful because she was able to establish that variation in the extent of association with escorts affects pups from the same litter.

Female lions (*Panthera leo*) form prides composed of closely related females (Packer *et al.* 1988; Packer & Pusey 1995). Prides must contain at least three adult females to be viable; smaller prides are unable to maintain their territories. Members of prides hunt together and vigorously defend their territories against intruders (Packer *et al.* 1990). Mothers of cubs also defend their cubs from attacks by infanticidal males (Packer *et al.* 2001). There are no dominance hierarchies in lion prides and all females reproduce equitably (Packer *et al.* 2001). Females give birth alone and are extremely secretive during the first few weeks after parturition. When cubs are five or six weeks old, they join other cubs in a 'crèche' and remain part of the crèche until they are approximately 18 months old (Packer & Pusey 1995). Cubs continue to nurse primarily from their own mothers, but are sometimes nursed by the mothers of other cubs in the crèche (Pusey & Packer 1994; Packer & Pusey 1995). The extent of allonursing increases as the degree of relatedness within crèches increases, and females who do not have cubs in the crèche do not participate in their care.

Female lions' reproductive success is positively related to the number of other mothers who have cubs in the crèche. In the Serengeti, where the availability of food varies seasonally, solitary females cannot raise large litters as successfully as females living in prides can (Packer & Pusey 1995). Moreover, cubs are more likely to survive when there are more mothers who have given birth at about the same time and when cubs are raised in crèches with many cubs of the same age (Packer & Pusey 1995; Packer *et al.* 2001). Cubs reared in crèches do not receive more milk than cubs reared alone, hence these effects are likely to reflect the benefits derived from communal defence against infanticide (Pusey & Packer 1994), which is a major cause of cub mortality (Pusey & Packer 1994).

In most of their range, Eurasian badgers (*Meles meles*) are solitary (da Silva *et al.* 1994; Johnson *et al.* 2000; Carpenter *et al.* 2005). But in some locations in the United Kingdom, badgers live in groups composed of one or more males, one to six closely related females and their offspring (da Silva *et al.* 1994; Woodroffe & Macdonald 2000; Carpenter *et al.* 2005). Group members share a den, but forage alone. For badgers in the United Kingdom, which feed mainly on earthworms, sociality may be a response to a patchy distribution of shareable resources (Johnson *et al.* 2000). Plural breeding occurs in badger groups, but not all females give birth each year. Older females reproduce more successfully than younger females, but there is no evidence of systematic reproductive suppression of individual females. When females live in groups, births are loosely synchronized and females who do not have cubs of their own provide care for the offspring of other females.

The size of social groups has no significant effect on the average reproductive success of females, but the rates of female reproductive failure seem to be higher in group-living populations than in solitary populations of badgers (da Silva *et al.* 1994). It is not clear whether these differences reflect the costs of living in social groups or differences in environmental conditions across populations. Woodroffe & Macdonald (2000) found that the number of cubs that survive to 1 year of age is positively related to the number of available helpers, but this effect seems to be an artefact of variation in territory quality. Groups that occupy high-quality territories contain more non-breeding females, more yearlings and more surviving cubs than groups that occupy lower quality territories. When the effects of territory quality are controlled statistically, the number of available helpers has no effect on the number or proportion of cubs that survive their first year of age. Woodroffe and Macdonald argue that females in large groups suffer more competition for resources than females in smaller groups, and this competition depresses their fat reserves and induces reproductive failure. This process creates more non-breeding females in larger groups. This interpretation is supported by the observation that the body condition of mothers is markedly worse when they live in groups with non-breeding females than when they live in groups without non-breeding females.

Black-tailed prairie dogs (*Cynomys ludovicianus*) live in extensive burrow systems ('towns') which are subdivided in wards and coteries (Hoogland 1981, 1983; Hoogland *et al.* 1989). Coteries typically include one adult male, three or four closely related adult females and their offspring. Mothers give birth in isolated nests and rear their pups alone for several weeks. Females respond aggressively when intruders attempt to approach their nests during this period. Maternal protectiveness is probably a response to infanticide, which is common in prairie dogs. The main perpetrators of infanticide are other lactating females, often close kin (Hoogland 1985). Pups emerge from their mothers' burrows when they are approximately four to six-weeks-old, and then begin to mix with pups from other coteries. Females may sleep with and sometimes nurse other females' pups during this phase (Hoogland *et al.* 1989). The annual reproductive success of adult females is negatively related to the size of the coterie in which they live (Hoogland 1981, 1983). If females are better off in smaller coteries than large ones, then they might be expected to emigrate to smaller coteries or establish new ones. However, females' dispersal options may be constrained because suitable unoccupied burrows are scarce in prairie dog towns and the costs of establishing new burrow systems for individuals is prohibitive.

(c) *Singular breeding with cooperative care of young*

In singularly breeding species with cooperative care of young, there is a considerable amount of reproductive skew. This complicates efforts to assess the effects of group size on reproductive success because group members may derive disparate benefits from group living. When non-breeding group members are closely related to the breeding pair, they may accrue inclusive fitness benefits from helping, but help is not limited to relatives in all cooperatively breeding mammals (Clutton-Brock 2002). Most analyses focus on the effects of group size on the number of offspring produced or offspring survival, emphasizing the fitness consequences for the breeding pair rather than non-breeding group members.

Although red fox (*Vulpes vulpes*) are primarily solitary, they sometimes form pairs or larger groups (Macdonald 1979; Zabel & Taggart 1989; Baker *et al.* 1998, 2004). In high-density populations in the United Kingdom, red fox typically form groups consisting of one dominant male, one dominant female, several subordinate adults and immature offspring (Baker *et al.* 1998). Most groups include some closely related adults, but the degree of relatedness within groups is relatively low because both males and females frequently mate with partners from outside the group (Baker *et al.* 2004). Dominant females monopolize reproduction, but subordinate females sometimes become pregnant and produce litters. However, dominant females live longer and have more offspring than subordinate females. Non-breeding adults guard, retrieve, provision, groom and play with pups (Macdonald 1979). In a sample of seven litters, pup survival was unrelated to the size of the group or the number of adult females in the group (Baker *et al.* 1998).

Dwarf mongoose (*Helogale parvula*) live in stable groups that typically consist of a single breeding pair, several offspring from previous litters and a few unrelated immigrants (Rood 1990; Creel & Waser 1991, 1994). The group forages and travels together, and shares a den. Subordinate females sometimes become pregnant, but rarely rear their litters successfully. Breeding females produce several litters of one to six pups over the course of the six-month birth season. Group members, including unrelated immigrants, take turns guarding pups in the den, bringing them insects and transporting them from one den to another. After pups emerge from the den, older pack members dig up insects for them and protect them from predators. Subordinate females, who have produced litters or experienced a pseudopregnancy, may lactate and nurse pups of the dominant female. There seem to be several advantages associated with living in larger packs. Adult mortality is lower in large groups than in small groups. Breeding females who have more helpers are also able to spend more time feeding (Creel & Creel 1991). Moreover, pups grow faster and are more likely to survive in large packs than small ones (Creel & Creel 1991). Packs above the median size produce on average 3.8 surviving pups, while packs below the median size produce on average 1.8 surviving pups. This relationship could be an artefact of variation in environmental conditions that influence both pack size and pup survival. However, analyses based on annual changes in group size and reproductive success within packs indicated that pack size has a direct effect on offspring survival (Creel & Waser 1994).

Meerkats (*Suricata suricatta*) in the Kalahari desert live in groups that are typically composed of a dominant breeding pair and 3–20 non-breeding helpers (Clutton-Brock *et al.* 2001; Russell *et al.* 2002, 2003). The dominant pair produces approximately 80% of all offspring born in the group; when subordinate females do breed, their offspring suffer high levels of mortality, probably due to infanticide. Females produce litters of three to six pups and may give birth to several litters per year. Helpers guard pups in the den, and then help feed them from the time they emerge from the den until they begin to forage independently at approximately three months of age.

There is no simple relationship between the size of social groups and offspring survival in meerkat groups. Clutton-Brock and his colleagues (1999) compared the effects of group size on pup survival to six months at two sites in the Kalahari. One site was located within the Kalahari Gemsbok National Park and the other was located on a fenced ranch. The density and diversity of predators was substantially higher in the park than on the ranch, but the sites were otherwise very similar. Rates of mortality between birth and weaning when pups are inside the den were similar at the two sites, but rates of juvenile and adult mortality were considerably higher in the park than on the ranch. The effect of group size on juvenile mortality also differed at the two sites. Juvenile mortality declined with increasing group size in the park, but showed the opposite pattern on the ranch. Clutton-Brock *et al.* suggested that the most likely explanation of the negative relationship between group size and mortality in the park was that helpers provided less effective defence of juveniles when the ratio of helpers to pups was low. If this argument is correct, then the ratio of pups to helpers may be more important than the absolute number of helpers. Subsequent studies of meerkats in the Kalahari confirm the importance of the ratio of pups to helpers in meerkats.

The presence of helpers has no effect on female litter size or on the survival of infants between birth and weaning among Kalahari meerkats (Clutton-Brock *et al.* 1999; Russell *et al.* 2002, 2003). However, after pups emerge from the den, the effects of helpers become apparent. The ratio of pups to helpers is significantly related to the rate of daily food intake for pups and their daily weight gain (Russell *et al.* 2002, 2003). Experimental manipulations of the ratio of pups to helpers confirm the causal link between help and pup growth rates. Thus, when experimenters temporarily removed pups from their packs, and decreased the ratio of pups to helpers by 75%, daily weight gains increased. Similarly, when experiments temporarily added pups to packs and increased the ratio of pups to helpers by 75%, pup weight gains declined. The effects of helpers on daily weight have important downstream effects: daily weight gains are related to juvenile weights, juvenile survivorship, the chance of breeding as subordinates and acquiring dominant status (Clutton-Brock 2002; Clutton-Brock *et al.* 2001).

The number of helpers in the group also has direct effects on females' reproductive success (Russell *et al.* 2002, 2003). Approximately 43% of all litters fail completely; none of the offspring survive to weaning. Litter failure is mainly a function of maternal status: 16% of the litters produced by dominant females failed completely, while 77% of the litters produced by subordinate females failed completely (Russell *et al.* 2003). For litters in which at least one pup survived to weaning, litter size at weaning was significantly related to maternal weight and the number of helpers. Heavier mothers with more helpers raised more offspring to the age of weaning than lighter mothers with fewer helpers (Russell *et al.* 2003). However, pup survival showed a 'bell-shaped distribution with group size' (Russell *et al.* 2002), as pups in the smallest and largest groups were less likely to survive than pups in intermediate-sized groups. Helpers also reduce the costs of maternal investment. The number of helpers present is negatively related to the length of subsequent interbirth intervals, and positively related to females' weight at the next conception. Female weight at conception is, in turn, positively related to litter size. Thus, helpers make it possible for females to increase their reproductive output without jeopardizing their condition.

Black-backed jackals (*Canis mesomelas*) are omnivores that live in brush land habitats (Moehlman 1979). They form stable pair bonds and cooperatively defend their territories, hunt and share food. Groups are usually composed of a single breeding pair, their offspring and several adult helpers who are believed to be offspring from previous litters. Helpers regurgitate food for lactating females and guard, play, groom and feed pups. Pups spend less time alone at the den in groups with larger number of helpers. Although some pairs are able to raise offspring without helpers, the number of surviving pups is closely related to the number of helpers. The incremental effect of each helper is equivalent to 1.5 pups.

Wolves (*Canis lupus*) in northern Minnesota live in packs that are composed of one breeding pair and their descendants (Harrinton *et al.* 1983). Non-breeding group members help care for pups, providing them with food and protection. Starvation is the main natural cause of mortality for wolf pups, hence the presence of helpers could have a substantial impact on pup survival. Harrington *et al.* (1983) monitored a number of packs at two different sites. At one site, prey density was high and population size was increasing. There, the number of non-breeding adults in packs was positively correlated with the number of surviving pups. In the other population, there had been a major decline in prey availability and the population size was declining. In the packs at this site, there was a non-significant negative relationship between the pack size and the number of surviving pups.

African wild dogs (*Lycaon pyctus*) live in groups that typically include one breeding pair, a number of non-breeding adults and offspring from several litters (Malcolm & Marten 1982; Creel & Creel 2002). Packs sometimes include adults that are unrelated to the breeding pair (McNutt 1996). Males are philopatric and females disperse with other females from the same litter (Malcolm & Marten 1982). Females produce one litter per year of about eight pups (Creel & Creel 2002). All group members, including those who are unrelated to other group members, help care for pups. Helpers regurgitate meat for pups that are too small to travel to kills and protect pups from predators. In times of food shortages, yearlings may not regurgitate for pups and sometimes appropriate food that is brought back to the den for pups. In contrast, adult dogs continue to regurgitate for pups even when food is scarce. Using data from three different sites, Creel & Creel (2002) demonstrated that the number of surviving pups is positively related to the number of adults in packs. However, pup survivorship is reduced in both exceptionally small and exceptionally large packs.

Cooperative breeding occurs in several genera of the primate family, Callitrichidae (*Callithrix*, *Leontopithecus* and *Saguinus*). These animals live in small, territorial groups of 4–15 individuals (French 1997; Tardif 1997; Bales *et al.* 2000, 2001; Dietz 2004). Unlike other anthropoid primates, callitrichid females typically give birth to 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). Females would be unable to sustain these costs without substantial help from other group members.

Breeding is monopolized by the dominant female in the group (French 1997; Tardiff 1997; Dietz 2004). This reproductive monopoly is sometimes the product of social suppression of reproductive physiology and sometimes the result of inbreeding avoidance (Saltzman *et al.* 2004*a*,*b*). In common marmosets, subordinate females were only able to rear litters if they gave birth when the dominant female did not have dependent infants (Digby 1995). In several cases, dominant females have killed infants produced by subordinate females (Digby 2001). In golden lion tamarin groups (*Leontopithecus rosalia)* approximately 10% of females share reproduction with subordinate females temporarily. Females are most likely to share breeding with their own daughters, less commonly with sisters and rarely with unrelated females. Only mothers and daughters were both successful in rearing infants in the same season (Dietz 2004). Although the number of surviving infants per female is lower in groups in which two females breed than in groups in which only one female reproduces (Dietz & Baker 1993), demographic models suggest that the cost of allowing daughters to breed is relatively low when unrelated mates are available and daughters do not pose a threat to mothers' social status within their groups.

Genetic analyses of group composition are now available for a small number of wild callitrichid groups. Some groups represent a single nuclear family, while others include adults that are unrelated to the dominant breeding pair (Nievergelt *et al.* 2000; Faulkes *et al.* 2003; Huck *et al.* 2005). In most groups that have been observed, helpers provide care for all group infants and do not seem to discriminate on the basis of relatedness (Dietz 2004; Fite *et al.* 2005).

In free-ranging populations of callitrichids, the presence of helpers, particularly adult males, is positively related to females' reproductive success. In moustached tamarins (*Saguinus mystax*) and common marmosets (*Callithrix jacchus*), the number of adult males, but not overall group size, is positively associated with the number of surviving infants (Garber *et al.* 1984, Koenig 1995), but not overall group size. In golden lion tamarins, groups with two adult males raise more surviving infants than groups with just one adult male. The fact that infant survival is more closely tied to the number of adult males than to overall group size suggests that the effects on infant survival are not an artefact of variation in territory quality. However, it is not entirely clear why infant survivorship is more closely related to the number of adult males than to overall group size. It is possible that adult males play a more important role in rearing offspring than adult females or juveniles members do. Bales *et al.* (2000) suggest that differences in the experience of helpers may contribute to these findings. They found that the number of adult males had a more consistent effect on infant survival in newly established groups than in long-established groups of golden lion tamarins, which had more experienced helpers. If the populations that Garber *et al.* and Koenig surveyed happened to include a substantial number of recently established groups, their results may be influenced by the experience of potential helpers.

Studies of cooperatively breeding rodent and primate species suggest that the benefits of helpers are greatly attenuated under captive conditions. In the wild, Mongolian gerbils (*Meriones unguiculatus*) form groups that include one breeding pair and a number of subordinates (Ågren *et al.* 1989, cited in French 1994). French (1994) reared pairs of experienced Mongolian gerbils in small indoor cages with and without juvenile helpers. When juveniles were present, they helped their parents make nests and tend pups. However, the presence of juvenile helpers has no consistent effect on litter size, offspring survival, pup group rates or the length of interbirth intervals. Pine voles (*M. pinetorum*), which are found throughout eastern North America, also form extended family groups with a single breeding pair (Solomon *et al.* 1998). Powell & Fried (1992) examined the effects of juveniles on the growth and development of younger siblings in small outdoor enclosures. One pair of adults was placed in each enclosure and allowed to rear one litter. When the next litter was born, juveniles were removed to create families with zero to three juvenile 'helpers'. The number of juveniles present did not significantly affect pup growth rates or pup survival to 21 days of age, but interbirth intervals were significantly shorter in groups with three juveniles than in groups with smaller numbers of juveniles. Pups spent significantly more time alone in groups that had no juveniles than in groups in which juveniles were present. Similarly, although helpers reduce the costs of rearing offspring for callitrichid parents, especially fathers, housed in the laboratory (Price 1992; Santos *et al.* 1997; Fite *et al.* 2005), the number of juvenile helpers available does not seem to affect infant survival (Jaquish *et al.* 1997).

3. EFFECTS OF GROUP COMPOSITION ON FEMALES' REPRODUCTIVE PERFORMANCE

The benefits that females derive from living in social groups may be influenced by the characteristics of the other members of their groups. Strong biases in favour of female philopatry among mammalian species are generally attributed to the inclusive benefits derived from living with relatives. If so, the kin composition of social groups is expected to be related to females' reproductive performance.

A considerable amount of information about the effects of group composition on reproductive performance in rodents is derived from studies that were designed to evaluate mechanisms underlying the 3–5 year cycles in population density that characterize many microtine rodent populations. Charnov & Finerty (1980) hypothesized that cycling population dynamics might be the product of kin selection. They reasoned that kin selection will favour greater tolerance towards kin than non-kin, and this would therefore encourage association among kin. If animals settle near their relatives, clusters of closely related animals will develop. Tolerance among closely related animals will enhance the reproductive success of individuals and produce higher rates of population growth. However, as population density increases and suitable territories become scarce, animals will be forced to disperse over greater distances. Long-distance dispersal will lower the average degree of relatedness among animals that occupy neighbouring territories. This will lead to higher levels of aggression between individuals, suppress reproduction and reduce population density.

Three empirical predictions derived from the model are of particular interest here: (i) animals will associate preferentially with relatives, (ii) the presence of kin will reduce levels of competition, and (iii) association with relatives will enhance female reproductive performance. A number of studies of voles were designed to test these predictions. Researchers focused on the effects of kinship on the behaviour of females because male voles typically disperse over greater distances than females (Ims 1989; Ylönnen *et al.* 1990; Lambin & Krebs 1993; Lambin & Yaccoz 1998; Dalton 2000). The model is usually tested by establishing enclosed populations composed of kin or non-kin and appropriate numbers of adult males, and monitoring patterns of population growth, infant survivorship and females' reproductive performance. In most of these experimental studies, movement into the study populations is prevented and predators are excluded.

A number of vole species, including meadow voles (*M. pennsylvanicus*), grey-tailed voles (*M. canicaudus*), Townsend's voles (*M. townsendiia*), field voles (*M. agrestis*), red-backed voles (*Clethrionomys rofocanus*) and bank voles (*C. glareolus*), have very similar social organizations (Wolff 1994). In these species, females sometimes form huddling groups during the winter to reduce thermoregulatory costs. But as temperatures rise in the spring, females generally establish individual home ranges and rear their young alone. Females usually settle near their natal territories, while males disperse further (Boonstra *et al.* 1987). In these species, males' ranges overlap the territories of multiple females. Males do not help females build or maintain nests and do not tend offspring, and females may mate with multiple males (Gruder-Adams & Getz 1985; McGuire & Novak 1986; Oliveras & Novak 1986; Boonstra *et al.* 1993; Spitzer *et al.* 2005). Females defend their home ranges against intruders (Mappes *et al.* 1995) and may not begin to breed until they have established individual home ranges (Kawata 1986).

One of the first studies designed to test the Charnov–Finnerty hypothesis was conducted on meadow voles (*M. pennsylvanicus*). Boonstra & Hogg (1988) monitored the rate of population growth in one enclosure stocked with three sisters and their daughters and a second enclosure that was stocked with an equal number of unrelated females. Females in the kin enclosure were 16% more likely to carry pregnancies to term than females in the unrelated enclosure. Some litters were located by tracking females back to their nests from the trapping sites. Litters of females in the kin enclosures were approximately 13% larger than the litters of females in the non-kin enclosure. In addition, a significantly larger proportion of infants from the litters located in the kin enclosure survived and were subsequently trapped than in the non-kin enclosure. However, the number of surviving offspring per litter was about the same in the two treatments. By the end of the six-month experiment, both enclosures had reached extremely high densities and population sizes were roughly equal, leading Boonstra and Hogg to conclude that 'relatedness among females had no effect on demography', and to dismiss the differences in reproductive parameters in the two enclosures as statistical anomalies.

Dalton (2000) also found that relatedness among female grey-tailed voles had no consistent effect on females' reproductive performance. Dalton seeded each of eight enclosures with six unrelated adult females and six unrelated adult males. Four enclosures were not manipulated further and relatedness was allowed to build-up through recruitment. In the other four enclosures, juveniles were removed from their natal enclosures and replaced with juveniles of the same age and weight from other enclosures. This procedure maintained population size, but prevented levels of relatedness from building up. Over the course of the six-month study period, there were no significant differences in the reproductive performance of females in the two groups.

Other studies of voles suggest that the presence of kin may increase female tolerance and enhance reproductive performance. In experimental enclosures, females tend to settle closer to their relatives than to non-relatives (Kawata 1986; Lambin & Krebs 1993; Pusenius *et al.* 1998), and their home ranges overlap more with their relatives than with non-relatives (Wolff *et al.* 1994; Mappes *et al.* 1995). In some cases, settlement near kin facilitates the establishment of individual home ranges (Kawata 1986) and earlier initiation of reproductive activity (Pusenius *et al.* 1998). In several experimental studies, females who settled near kin reared higher numbers of surviving offspring than females with no close kin nearby (Kawata 1990; Ylönnen *et al.* 1990; Mappes *et al.* 1995; Lambin & Yaccoz 1998; Pusenius *et al.* 1998; Wolff *et al.* 2002). In one study, which was allowed to continue across years, females who settled near close kin were more likely to survive from one year to the next (Lambin & Krebs 1993).

The mechanisms underlying observed differences in reproductive performance between females living near kin and females living near unrelated females are not well established. However, living near kin seems to reduce the intensity of competition with conspecifics. In enclosures that are seeded with unrelated females, females' reproductive success increases as their distance from their nearest neighbours increases. In contrast, when kin are present, the distance to nearest neighbours has no effect on females' reproductive success (Mappes *et al.* 1995; Pusenius *et al.* 1998). Analyses of trapping patterns suggest that subordinates may be less intimidated by the presence of dominant individuals when enclosures are seeded with groups of relatives than when they are seeded with non-kin (Ylönnen *et al.* 1990). In these vole species, living near kin may lower levels of aggression, reduce the extent of competition for resources or lower the risk of infanticide (Dalton 2000). Such competition may have important effects on females' ability to rear young successfully. Juvenile survivorship generally declines as female density increases (Rodd & Boonstra 1988). In one study, juveniles were reared in groups that differed in the ratio of mature males to mature females. The survival of juvenile females was lower and age to maturation was later in groups with a female-biased sex ratio than in groups with an even sex ratio or a male-biased sex ratio (Wolff *et al.* 2002).

In wild populations of cooperatively breeding prairie voles, group composition influences females' reproductive performance. Females that lived in groups composed of three adults reared more surviving pups than females who lived in smaller or larger groups (McGuire *et al.* 2002), but females reproduced most successfully when they lived in groups with two other adult males and no other adult females. Information about the relatedness of females in groups that contained more than one adult female was not available in this study, but captive studies suggest that the costs of reproduction may be reduced when related females are present. Sera & Gaines (1994) compared female prairie voles housed in enclosures with familiar littermate sisters or with unrelated females. When females were housed with kin, their homes ranges were larger and overlapped more with the home ranges of neighbouring females. Females who were housed with kin were significantly more likely to have multiple pregnancies each season than females housed with unrelated females. However, these differences were not reflected in differences in the number of surviving offspring produced per female. Hayes & Solomon (2004) compared the breeding success of females in groups composed of two adult littermate sisters and one unrelated adult male with the breeding success of females housed with a single adult male under conditions of high and low food availability. In this experiment, litter size was adjusted so that all litters were composed of three pups. In some of the groups that contained sisters, both females produced litters and pooled their litters. Litters from plurally breeding groups weighed significantly more at the end of the lactation period than litters from groups that contained only one adult female; litters from groups composed of one breeding and one non-breeding female fell between the two extremes. Mothers in plurally breeding groups spent less time nursing pups than mothers in groups that included just one female. In addition, mothers in plurally breeding groups were able to maintain their body weight over the course of lactation when food was limited, while mothers in groups that included just one female lost weight. Mothers in groups in which only one of the two females reproduced experienced intermediate weight losses and nursing levels.

White-footed mice (*Peromyscus leucopus*) and deer mice (*P. maniculatus*) are sympatric in the southern Appalachian Mountains of Virginia. In both species, mothers typically nest alone and rear one litter at a time at low densities, but when densities increase female dispersal is delayed and extended family groups are formed (Wolff 1994). Male deer mice are more fully involved in offspring care than male white-footed mice (Wolff & Cicirello 1991). Wolff (1994) monitored the reproductive performance of female deer mice and white-footed mice that nested in artificial nest boxes and evaluated the effects of group composition on their reproductive performance. Some females nested alone (solitary), with juveniles from previous litters (extended family), with other breeding females (communal) or with other breeding females plus juveniles from previous litters (communal-extended). When communal breeding groups were formed, they typically consisted of mothers and daughters or sisters. There was no effect of the type of social group on the number of weanlings raised or the number of offspring that survived to six weeks, the median age of dispersal for juveniles. Solitary female white-footed mice had shorter residence in nest boxes than females that lived in communal-extended groups, but there was no consistent effect of group size on residence times in deer mice. Thus, living in extended family groups and nesting communally had no positive or negative effects on females' reproductive performance. Wolff (1994) suggests that extended families and communal nesting represent 'alternative breeding tactics in response to limited breeding space (usually in response to high density conditions)…Social tolerance of relatives may be an adaptation that provides offspring with extended parental care during times of environmental or social uncertainty'.

Commensal house mice (*Mus musculus*, *M. domesticus*) typically form groups composed of one male, one or more breeding females and their litters. Females nearly always pool their litters if they are born about the same time and nurse them communally (König 1994*a*,*b*; Hayes 2000). Several lines of evidence suggest that females preferentially nest with close kin. In wild populations, females are more closely related to other females in their own groups than to females in other groups (Saltzman *et al.* 2004*b*). Females prefer to nest with females that have similar major histocompatibility complex (MHC) alleles, and MHC similarity is a reliable correlate of genetic relatedness (Manning *et al.* 1992). Females are more likely to form associations and nest communally in semi-natural enclosures seeded with groups of sisters than in enclosures seeded with unrelated, unfamiliar females (Dobson *et al.* 2000; Rusu & Krackow 2004).

Associations with familiar partners also confer reproductive benefits on females. König (1994*a*,*b*) compared the reproductive performance of females over a standardized lifespan of 120 days when they were housed alone, housed with littermate sisters and housed with unrelated, unfamiliar females. The lifetime reproductive success of females housed with sisters was on average 25% higher than the lifetime reproductive success of females housed with unrelated females and 30% higher than the lifetime reproductive success of females housed alone. There is also evidence that reproduction is more egalitarian when females form associations with kin than when they form associations with non-kin. Dobson *et al.* (2000) compared groups composed of two or three littermate sisters with groups composed of two or three unrelated, unfamiliar females. When females were housed with sisters, all females produced offspring. However, when females were housed with unrelated females, one female in each group failed to reproduce. There was no difference in litter size among breeding females housed with sisters and unrelated females, but the level of mortality during the interval between birth and weaning was significantly lower when females were housed with sisters than when females were housed with unrelated females. Mortality between birth and weaning was mainly due to infanticide, although it is not known if pups were killed by nesting females or adult males.

The dynamics of population outbreaks among feral house mice in Australia also suggest that associations with kin enhance females' reproductive performance (Sutherland *et al.* 2005). Early in the cycle, population size is low and females maintain separate home ranges. Related females tend to be found in neighbouring home ranges. As the size of the population increases, the extent of kin clustering becomes more pronounced and related females share home ranges. Females selectively interact with their relatives. At the peak of the population outbreak, kin structuring breaks down, but females continue to interact preferentially with close kin. Sutherland and colleagues suggest that association with kin reduces vulnerability to infanticide, thus increasing rates of recruitment and population size.

Bushy-tailed wood rats (*Neotoma cinerea*) live on discrete rocky outcrops in mountainous areas of North America (Moses & Millar 1994). There are a limited number of suitable nest sites and this may create considerable competition among females. Females tend to remain on their natal outcrop throughout their lives. Mothers and daughters are frequently found in the same locations within the outcrop and are more likely to be found together than unrelated females are. For mothers, there were no apparent effects of having daughters nearby. Mothers reared as many offspring when daughters were present as they did when there were no daughters present. But females whose mothers are present have larger litters and fewer litter failures than females whose mothers are not present. Moreover, females are more likely to survive their first winter when their mothers are present than when their mothers are absent. Differences in daughters' survival disappear when population density is experimentally reduced, which suggests that mothers enhance their daughters' survival by reducing the intensity of competition for resources.

Wood mice (*Apodemus sylvaticus*) reproduce alone or in communal groups of two related or unrelated females (Gerlach & Bartmann 2002). Gerlach and Bartmann compared the reproductive performance of females housed in small indoor enclosures under four different conditions: (i) one female alone, (ii) mother–daughter pairs, (iii) two familiar sisters, and (iv) two unrelated, unfamiliar females. When females were housed in pairs, one of the females generally produced about twice as many offspring as the other female. The more successful of the two females in communally breeding groups produced as many offspring as females that bred alone, while the less successful of the two females produced significantly fewer offspring than females that bred alone. However, females do gain some advantages from breeding communally. Females that were housed in pairs spent significantly less time nursing than females who bred alone. This might enable communally breeding females to conserve energy for future reproductive attempts. It is not clear whether the energetic benefits of reproducing in communally breeding groups outweigh the costs of reduced fertility for all females in more natural circumstances.

Alpine marmots (*M. marmota*) live at high elevations in areas with short growing seasons and long, harsh winters. They form extended family groups that are typically composed of a dominant breeding pair, offspring from several litters and some unrelated individuals (Arnold 1990; Allainé 2000). Juveniles delay dispersal for several years after reaching maturity (Allainé 2000). The dominant female produces all offspring born in the group, although all mature females come into oestrus. Most, but not all offspring, are sired by the dominant male in the group (Hackländer *et al.* 2003). Infants are particularly vulnerable to thermoregulatory stress during their first winter because they have accumulated relatively little fat by the time the winter begins, and their small body size and high surface to volume ratio increases the rate of heat loss. Thermoregulatory stress is reduced by huddling together during hibernation (Hayes 2000). Infants are more likely to survive their first winter in groups in which most individuals are closely related than in groups in which most individuals are not closely related (Arnold 1990). Moreover, mortality is lower in groups that contain a breeding pair and other adults than in groups that contain a breeding pair and yearlings or a breeding pair alone. There is some evidence that living with unrelated females can be costly for breeding females. Thus, the reproductive success of dominant females is negatively related to the number of unrelated subordinate females in the group, but is not affected by the number of daughters present (Hackländer *et al.* 2003).

Grey seals (*Helichoerus grypus*) forage at sea and come ashore to mate, give birth and nurse their young. Females tend to return to the same sites each year and some females return to their natal sites to breed (Pomeroy *et al.* 2000, 2001). Genetic analyses indicated that females that occupied certain breeding locations were more closely related to the colony as a whole than females that occupied other breeding locations (Pomeroy *et al.* 2001). Females that occupied these areas of higher than average relatedness produced larger and faster growing pups than females that occupied other locations. Since larger pups are more likely to survive than smaller pups, females that bred in these favoured locations may achieve higher reproductive success and contribute more to the genetic composition of the colony than other females. The combination of high site fidelity and site-specific variation in reproductive performance could create the observed genetic structuring of the population, even if associations among females were entirely passive. This does not seem to be the case. Although females showed considerable site fidelity, some did shift their pupping locations from one year to the next. Using a model based on random patterns of association, Pomeroy *et al.* (2005) demonstrated that the likelihood of association among mothers that shifted their pupping locations substantially is much greater than expected by chance. These data indicate that particular pairs of females actively coordinate their movements. Pomeroy *et al.* (2005, p. 533) speculate that 'Familiarity may then lead to behavioural modifications between the individuals concerned, which ultimately produce some measurable fitness benefit, either in reduced costs to the mother or increased performance in raising offspring. Likely possibilities include reduction of aggression between familiar associates, or preferential access to limited resources'.

Female African elephants (*Loxodonta africana*) live in complex fission–fusion societies. Females form stable core groups which consist of 1–20 adult females and their offspring. Females typically remain in their natal core groups when they mature, while males disperse. These core groups may temporarily fragment into smaller parties and multiple core groups may join to form large aggregations. Some pairs or trios of core groups consistently associate together and are said to form a 'bond group' (Moss & Poole 1983; Moss 1988). Recent analyses indicate that the average level of genetic relatedness among females within core groups is approximately 0.15, just higher than expected for aunts and nieces (Archie *et al.* 2006). Analyses of the patterns of association among females indicate that kinship also predicts the patterns of association among females within bond groups. Females who spend most of their time together are generally first-order relatives. Members of bond groups are related through the matriarchs of the core groups. The long-term stability of core groups may have important reproductive consequences for females. Females who belong to core groups led by old matriarchs have significantly higher reproductive success than females who belong to core groups led by younger matriarchs (McComb *et al.* 2001).

Studies of howler monkeys (*Alouatta* spp.) also demonstrate that the composition of social groups influences female reproductive performance. In red howler (*A. seniculus*) groups, the number of adult females in groups is confined within relatively narrow limits. Most groups contain two to four adult females (Treves 2001). Groups with too few females cannot defend their territories, while groups with too many females face more competition for access to resources and become more attractive targets for male takeovers (Pope 2000*a*). This means that female dispersal strategies are tightly linked to the number of adult females present: in mantled howler (*A. palliata*) groups with two adult females, 50% of all natal females disperse; in groups with three adult females, 90% disperse; and in groups with four adult females, 100% disperse (Crockett & Pope 1993; Pope 1998). Recruitment into the natal group is advantageous because females that mature and breed in their natal groups have higher quality diets and give birth at earlier ages than ones which emigrate (Crockett & Pope 1993). This creates competition for the limited number of breeding positions within established groups. Adult females actively harass maturing females in an effort to force them to emigrate, and recruitment opportunities are concentrated among the descendants of a single female (Pope 2000*b*).

Non-random recruitment of daughters of high-ranking females would generate an increase in the average degree of relatedness among breeding females over time. In fact, in long-established groups, females represent a single matriline and the average degree of relatedness approaches that of first degree relatives (Pope1998, 2000*a*,*b*). In newly established groups, which are composed of migrants from a number of different social groups, relatedness is approximately zero. The genetic composition of groups is associated with their reproductive performance. Females in newly established groups have fewer surviving infants per year than females in well-established groups do (Pope 2000*a*). These differences suggest that females benefit from living in groups of close kin, but it is also possible that differences in reproductive performance are linked to other factors, such as differences in territory quality.

In matrilineal primate species, females interact preferentially with close kin and selectively support close kin in agonistic encounters (Silk 2002, 2006; Kapsalis 2004). Although the presence of kin seems to have an important effect on females' everyday lives, the impact of the presence of kin on females' reproductive performance is harder to evaluate. In captive vervet monkeys (*Chlorocebus aethiops*), young females whose mothers are present are less likely to be harassed and more likely to be defended than females whose mothers have died. Females' firstborn infants are more likely to survive when the grandmother is present (Fairbanks & McGuire 1986). These effects are not confounded by differences in the dominance rank of females whose mothers are present and absent. Semi-free-ranging Japanese macaques, *M. fuscata*, produce their first infant at significantly younger ages and tend to have shorter interbirth intervals when their mothers are present in the group than when their mothers are dead (Pavelka *et al.* 2002). For wild baboons, the effects of mothers' presence on the reproductive success of their daughters seem to be less consistent. Thus, at Gombe in Tanzania, mothers' presence has no consistent effect on their daughters' age at menarche or the length of their interbirth intervals, or on their grandchildren's survival (Packer *et al.* 1998). In the Okavango Delta of Botswana, the daughters of high- and mid-ranking females produced their first infant at significantly younger ages when they had mothers or adult sisters in the group. For low-ranking females, however, the pattern was reversed (Cheney *et al.* 2004). The presence of mothers or adult sisters tended to reduce females' interbirth intervals, but did not influence infant survival, perhaps because infanticide is the main source of mortality for infants at this site.

4. EFFECTS OF SOCIAL BONDS ON FEMALES' REPRODUCTIVE PERFORMANCE

Very little is known about the relationship between the nature of social bonds and the females' lifetime fitness. One reason for this is that there is a taxonomic mismatch between the availability of information about social behaviour and fitness. The most complete information about female reproductive performance comes from studies of small, short-lived animals, like voles and house mice. Many of these studies are based on trapping data, which tell us little about the nature of interactions among females. We know much more about the social relationships among females in other taxa, including hyenas, elephants, sperm whales, lions and various species of primates (de Waal & Tyack 2003). Unfortunately, all of these animals are relatively large and long-lived, making it difficult to document the lifetime reproductive performance of sizable numbers of individuals. This creates a mismatch between the availability of information about social behaviour and the reproductive performance. However, we are beginning to make some progress in efforts to evaluate the adaptive value of social relationships for females in some primate taxa.

In their 1986 paper, Cheney and her colleagues focused on three kinds of relationships to provide examples of the 'possible function' of long-term social bonds in primate groups: relationships with close kin; close associations, or 'friendships', between adult male and females; and male–male alliances. Over the last 20 years, we have gained a considerably more complete understanding of the structure and function of these kinds of relationships. Much of this information comes from studies of baboons, which have been intensively studied over extended periods at multiple sites across Africa (Henzi & Barrett 2003; Swedell & Leigh 2006). These long-term studies provide a valuable database for testing adaptive hypotheses and an important source of information about the proximate and distal consequences of variation in sociality.

The first clue about the link between social bonds and female fitness came from analyses of the relationship between female dominance rank and reproductive success in primate groups. Like a number of other Old World monkeys (Chapais 1992) and spotted hyenas (*Crocuta crocuta*; Engh & Holekamp 2003; Engh *et al.* 2000), baboons form matrilineal dominance hierarchies in which maternal kin occupy adjacent ranks (Silk *et al.* 2003). In baboons, coalitionary support from relatives plays an important role in the acquisition of female dominance rank (Johnson 1987) and may also contribute to the extraordinary stability of female dominance hierarchies, even though coalitions among adult females are not common at all sites (Silk *et al.* 2003). High rank confers some short-term advantages on females. Thus, dominant females sometimes gain priority of access to food (Barton 1993) and high-ranking matrilines are more cohesive than low-ranking matrilines (Silk *et al.* 1999, 2004).

There may also be long-term benefits associated with high rank. High-ranking females' infants grow faster than lower ranking females' offspring do (Johnson 2003; Altmann & Alberts 2005) and their daughters reach menarche at earlier ages (Altmann *et al.* 1988; Wasser *et al.* 2004). High-ranking females also have shorter interbirth intervals (Bulger & Hamilton 1987; Rhine *et al.* 1988; Smuts & Nicholson 1989; Barton & Whiten 1993) and their infants are more likely to survive their first year of life (Bulger & Hamilton 1987; Rhine *et al.*1988; Silk *et al.* 2003; Wasser *et al.* 2004). In Mikumi, the lifetime reproductive success of females in the highest ranking quartile is about four times higher than the lifetime reproductive success of females in the lowest ranking quartile (Wasser *et al.* 2004). However, significant effects of female dominance rank on all of the components of female reproductive success are not observed in all baboon populations (e.g. Packer *et al.* 1995; Cheney *et al.* 2004) or during all periods (Altmann & Alberts 2005).

The biological significance of the moderate and seemingly inconsistent effects of dominance rank may be interpreted in several different ways. Packer *et al.* (1995) suggested that stabilizing selection on the kinds of traits that confer high rank on females, such as aggressiveness, might lower the fitness of the highest ranking females. It is also possible that most analyses are based on samples that are too small to detect the effects of dominance rank. A 5% selective differential can have powerful effects on the evolution of a trait, but very large samples would be required to detect a statistically significant effect of this magnitude. We also must consider the possibility that the effects of dominance rank may be swamped by other factors that are largely independent of dominance rank, such as predation or infanticide (Cheney *et al.* 2004). The effects of dominance rank may only be expressed under certain kinds of environmental conditions. In Amboseli, the effects of dominance rank on female reproductive performance were considerably more pronounced under harsh environmental conditions than under more benign conditions (Alberts & Altmann 2003; Altmann & Alberts 2003). In Mikumi, rank-related differences in reproductive performance disappeared during a period of drastic population decline (Wasser *et al.* 2004). Finally, it is possible that females adopt social strategies to compensate for rank-related disparities in reproductive success. For example, Henzi and his colleagues have shown that female baboons tend to direct more of their grooming towards higher ranking females during periods of food scarcity than when food is more abundant (Henzi *et al.* 2003). Females might also develop social strategies that insulate them from some of the costs of being low ranking.

Several lines of evidence suggest that social bonds among females play an important role in females' lives and may influence their reproductive performance. First, comparative analyses of baboon time budgets indicate that females preserve time for socializing (Dunbar & Sharman 1984). When food is scarce, females devote more time to foraging and moving between feeding sites. However, they do not reduce the amount of time that they spend interacting peacefully with other group members. Instead, they cut back on resting time. One interpretation of these findings is that females continue to groom group members when environmental conditions deteriorate because these relationships have enough value to females that they maintain them even under difficult conditions.

Second, the social lives of female baboons revolve around a tight core of close associates (Silk *et al.* 1999; Silk *et al.* 2006*a*,*b*). In Amboseli, females show pronounced preferences for close kin, including mothers, daughters and sisters. Females also prefer to groom and associate with unrelated age mates and those who are close to their own rank. But even in the absence of close maternal kin, most females form strong social bonds with at least one partner. Although demographic factors impose important constraints on the availability of preferred types of partners, some of the close social bonds that females form last for a number of years. Females tend to form the most enduring bonds with close kin and age mates. The quality of social bonds has a direct effect on their strength and stability. Females who groom most equitably have the strongest and most enduring social bonds, and these effects are independent of the degree of relatedness and age proximity among females.

Third, females respond strongly to the sudden loss of favoured companions. Engh and her colleagues analysed hormone levels in faeces collected from known female baboons in Moremi, Botswana (Engh *et al.* 2006*b*). They found that the levels of glucocorticoids rise sharply after the disappearance of close relatives. Nearly all of the disappearances were attributed to predators, hence Engh *et al.* considered the possibility that females' reactions reflect the stress of the predator attacks, not the loss of close companions. If that is the case, then all group members who survive attacks ought to react in the same way. However, only females who lose close kin show elevated glucocorticoid levels.

Fourth, females compensate for the loss of preferred partners by strengthening their relationships with others. Engh and her colleagues found that females increase the frequency and diversity of their grooming relationships after they lose close companions, suggesting that they attempt to compensate for their losses by forging new relationships. Similarly, females in Amboseli form stronger bonds with their maternal and paternal sisters when their mothers are not present than when their mothers are available (Silk *et al.* 2006*a*).

Female baboons may also gain important benefits from the relationships that they form with adult males. These kinds of relationships, sometimes labelled 'friendships', are a conspicuous feature of social life in baboon groups. After females give birth to infants, they often form close associations with one or sometimes two adult males (see Smuts 1985). Females are principally responsible for maintaining proximity to their male associates and groom males much more than they are groomed in return (Smuts 1985; Palombit *et al.* 1997). Males sometimes protect their female associates from harassment (Smuts 1985). Moreover, field playback experiments conducted in the Okavango Delta of Botswana indicate that males are more responsive to their female associates' distress calls than are unaffiliated males, and males respond more strongly to their female associates' distress calls than to the distress calls of other females (Palombit *et al.* 1997). If males' responses can be taken as evidence that they are prepared to intervene on behalf of their female associates or their infants, then the results of these experiments suggest that females gain protection for themselves and their infants from their male associates.

The value and scope of such protection may vary across sites. In Amboseli, where the risk of infanticide is apparently low, males preferentially support their juvenile offspring when they are involved in agonistic disputes (Buchan *et al.* 2003). Males' ability to recognize their offspring may be at least partly influenced by their previous associations with mothers and their infants. In southern Africa, where males often kill unweaned infants when they join new groups and acquire top-ranking positions, females' associations with males may protect their infants from infanticidal attacks (Palombit *et al.* 1997; Weingrill 2000; Palombit 2003).

This interpretation is supported by several lines of evidence from Moremi. First, lactating females typically respond fearfully to new males and attempt to avoid them. Males who have seemed indifferent to infants may abruptly change their behaviour towards infants sired during their tenure after they are deposed, carrying them on their ventrum when new males are in the vicinity. Second, lactating females' glucocorticoid levels rise substantially when new males join the group and acquire high-ranking positions (Beehner *et al.* 2005; Engh *et al.* 2006*a*). The fact that these effects are confined to lactating females suggests that females respond to the threats to their infants, not just to the presence of unfamiliar males. Moreover, lactating females' responses to the presence of potentially infanticidal males were influenced by their associations with adult males. Females who had established associations with adult males were much less distressed than females who had not established such associations.

The short-term benefits that females gain from their associations with other females and with adult males are reflected in females' reproductive performance. In Amboseli, females that are more fully socially integrated into their groups reproduce more successfully than other females (Silk *et al.* 2003). In this study, female social integration was measured in terms of the proportion of time that females spend in close association with other group members and grooming. Female reproductive success was measured as the proportion of infants that survive to 1 year, which is a major component of variation in lifetime fitness among baboon females in this population (Alberts & Altmann 2003; Altmann & Alberts 2003). A positive relationship between the extent of social integration and the reproductive success might also occur because some females lived in more favourable habitats or during more favourable time periods than others. These females might have been more social and reproduced more successfully than other females. However, the results remained unchanged when the measure of social integration was corrected to account for group membership and changes in environmental conditions over time.

The positive relationship between the extent of social integration and reproductive success observed in Amboseli might arise because high-ranking females have higher reproductive success and belong to larger matrilines than lower ranking females do. However, the relationship between social integration and reproductive success remains significant when dominance rank and lineage size are controlled statistically. In fact, when the sample is partitioned by dominance rank and the sociality index score, we find that the most social low-ranking females reproduce as successfully as the most social high-ranking females. Thus, sociality seems to insulate females from some of the costs of low rank.

5. SUMMARY AND CONCLUSIONS

Sociality influences female fitness in diverse ways. In general, there seems to be support for the observation of Clutton-Brock *et al.* (2001) that negative correlations between group size and fitness characterize species in which females rear their infants on their own and in species that rear their offspring communally. In cooperatively breeding species, with high reproductive skew, group size has clear positive effects on offspring survival and the reproductive success of breeders, but the effects on non-breeding helpers have not been assessed. This makes it impossible to draw firm conclusions about the effects of breeding systems on female fitness.

As expected from kin selection theory, the presence of kin generally enhances females' reproductive performance, although kinship does not provide blanket immunity from fitness-reducing behaviour. Prairie dogs sometimes nurse the pups of closely related females and sometimes kill them. Data from long-term studies of baboons suggest that social bonds may have a direct and positive effect on female fitness, but the causal mechanisms creating these effects and the generality of these findings are still unclear.

One of the most obvious lessons that readers will draw from this review is that there is a lot more work to be done. Our knowledge about the effects of the relationship between group size, group composition and social relationships on the fitness of females is incomplete for even the best-studied mammal species. It would be useful to be able to replicate the analyses of the relationship between group size and group composition in a larger number of species and a much wider range of taxa. If we were able to describe the shape of the function which describes the relationship between fitness and group size, we might be able to develop broader insight about the nature of forces that influence females' reproductive performance in different mammalian taxa.

The second lesson to draw from this review is that long-term studies of free-ranging populations provide an enormously valuable source of information about the adaptive consequences of sociality. It is no accident that the most valuable insights about the functional consequences of sociality come from studies of free-ranging populations, including red deer, Kalahari meerkats, yellow-bellied marmots, lions and savannah baboons, that span decades.

One lesson that I hope primatologists draw from this review is that there are valuable payoffs for venturing beyond the primate literature. Comparative analyses that extend beyond the primates provide more powerful tests of adaptive hypotheses. For example, the fact that various measures of brain size and group size are consistently related in primates, cetaceans, ungulates, carnivores and insectivores (references above) gives much greater weight to the finding. The mammal literature is also useful if we want to understand the function of traits that are uncommon in primates, but occur in other taxa, such as cooperative breeding, fission–fusion social organization or pair-bonding.

A lesson that mammalogists might take from this review is that there is a sizable gap in the state of knowledge about social relationships in primates and other mammals. Primatologists have compiled detailed information about the social behaviour of individuals in a broad range of species. Comparable data are largely unavailable for other mammalian taxa, even those that have been studied carefully for long periods. In the absence of such data, we cannot make meaningful comparisons between primates and other animals in a number of important dimensions. This is important for our understanding of the evolution of social cognition. The social brain hypothesis posits that social complexity has created selection pressures for larger and more complex brains. This hypothesis is consistent with evidence that brain and group size are associated in various taxa. However, group size may be a poor proxy for social complexity (Blumstein & Armitage 1998). Valid assessments of social complexity require more detailed information about the nature of social interactions among individuals than is available for most taxa.

The absence of such information makes it very difficult to make any systematic comparisons of the consequences of sociality, the extent of social complexity or the nature of social cognition in primates and other taxa. For example, we generally take it for granted that primates are more socially complex than other animals. However, it is not clear that we have a firm basis for this conclusion. Spotted hyenas establish matrilineal dominance hierarchies, form coalitions, reconcile after conflicts, recognize paternal kin, hunt cooperatively and recognize third party relationships (Holekamp & Smale 1991; Engh *et al.* 2000, 2005; Wahaj *et al.* 2001, 2004). African elephants can recognize the vocalizations of at least 100 other individuals (McComb *et al.* 2001) and bottlenosed dolphins form stable, multi-level alliances (Connor *et al.* 2001). Corvids may share many of the elements of the cognitive toolkit that underlies complex cognition (Emery & Clayton 2004).

While the long lives of some of our study animals and the short term of most research grants make it difficult to assess effects of sociality on the fitness of females, the data reviewed here suggest that it is possible to move beyond the phenotypic gambit. These studies give us some idea about how to approach this task in the field and in more controlled conditions in the laboratory. It is hoped that the body of work described here provides a foundation for further analyses of these questions.

This paper was written while I was a visitor in the Large Animal Research Group in the Department of Zoology at the University of Cambridge. While my resolve to venture out of the safe shallows of primatology into the depths of the mammalian literature is a direct result of many congenial lunchtime conversations with the members of LARG, they bear no responsibility for any errors that have found their way into this manuscript.

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