

Cooperative Care of Young in Mammals

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The provision of care to non-offspring in animal societies has attracted substantial scientific attention because of its apparent contradiction to the concept of individual selection. In mammals such cooperative care of alien young has been described for both non-breeding and breeding females. I first review the types of non-offspring care that are known from mammals and then discuss the actual and potential fitness benefits and costs for the donors and recipients of this cooperative behaviour. For many species, however, quantitative analysis is still missing. Non-offspring care provided by non-breeding individuals may best be explained by indirect fitness benefits due to improved reproduction of a related breeder under environmental conditions in which successful direct reproduction is not possible. Cooperative care of young among breeding females is also directed preferentially to non-descendant kin and may have evolved due to mutualistic benefits. Our current knowledge of mammalian cooperative care of the young raises questions that must be answered in order to fully understand the evolution of social behaviour.

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Conspecifics are a major environmental factor for most organisms because they are not only potential mating partners (in sexually reproducing species) but also partners in competitive and cooperative interactions. It is the special focus of scientists in the field of sociobiology and behavioural ecology to study such interactions among organisms. Ultimately these studies aim to analyse the adaptive value of social behaviour and the way in which it influences an individual's biological fitness.

A somewhat simplified definition of fitness is an individual's lifetime reproductive success, i.e. the relative number of offspring an individual produces that survive into the next generation. According to our understanding of the process of evolution, we expect natural selection to promote any behaviour that maximizes the number of (surviving) offspring that an individual can produce under a given set of environmental conditions [1, 2].

With this concept of natural selection in mind, sociobiologists have noted that in several species individuals invest time and energy in the care of non-offspring. Such behaviour has been intensively studied in social insects, where many or most individuals within a colony may even spend their entire life in caring for and rearing the young of another female (for reviews see [3–5]). Alloparental care has also been well studied in cooperative breeding birds, for example, in Florida scrub jays (*Aphelocoma coerulescens coerulescens*), acorn woodpeckers (*Melanerpes formicivorus*), white-fronted bee-eaters (*Merops bullockoides*) and groove-billed anis (*Crotophaga sulcirostris*; for reviews see [6–8]). In mammals, however, cooperative care has not yet been extensively analysed. Nevertheless, to develop models that explain the evolution of social behaviour in both invertebrates and vertebrates we must fill this gap by understanding the mechanisms that promote and stabilize such social cooperation in mammals.

The phenomenon of cooperative care

The use of terms to describe the phenomenon of non-offspring care is not uniform in the literature on vertebrates, although authors agree on the basic meaning. The following three examples illustrate this point (emphases added). According to Brown [7] a “*helper* (or *alloparent* or “*auntie*”) is an individual that performs parent-like behavior toward young that are not genetically its own offspring”; Creel and Creel [9] define “*communal breeding* to include all species in which individuals care for (guard, groom, carry, play with, feed, or nurse) offspring other than their own”; and Hoogland [10] suggests that “*cooperative breeding* – also known as *communal breeding* – occurs when breeding or nonbreeding individuals help conspecifics rear offspring.” For this concept I use the term cooperative care, in the sense given by Emlen [11]: “cooperative care refers to situations in which adult individuals in addition to the genetic parents regularly aid in the rearing of young”, which excludes paternal care towards young in monogamous mammals such as jackals and marmosets. Help provided by genetic parents is part of their parental investment and does not require further explanation.

Of approximately 4400 listed species of mammals 15% in seven orders show some form of cooperative care within social groups [12, 13]. Cooperative care in mammals includes direct interactions with non-offspring such as feeding, grooming, babysitting, helping infants in distress, assistance in thermoregulation, and allosuckling. Some authors also include more indirect activities that are likely to increase the breeding success of the recipient, for example, alarm calling in the presence of infants or provisioning a pregnant female [14]. Below I first describe the types of cooperative care that occur in mammals, discuss our current understanding of the evolution of such social behaviour, and then raise questions which may be helpful in advancing our knowledge of the benefits and costs of cooperative care.

Who provides cooperative care?

Within mammalian multi-female groups, reproduction is often distributed unequally among group members. In addition, there is intra-group variation among breeding females in the number of offspring raised; not every adult female is permitted to reproduce due to the structure of the reproductive dominance hierarchy. Such dominance hierarchies are gen-

erally an expression of intra-specific competition over limited resources such as food or nest places [15–17]. Vehrencamp [18] introduced the term ‘reproductive skew’ for the degree to which a dominant individual monopolizes overall reproduction in the group. In high-skew societies direct reproduction is concentrated in one or only a few dominant individuals; in low-skew societies reproduction is distributed more evenly among individuals. In mammals, as in birds and invertebrates, we observe a continuum from slightly skewed societies (in which several females share reproduction within a group) to strongly skewed societies, in which only one female breeds per group (despotic societies). The relevance for our discussion of cooperative care is that individuals that aid group members in the rearing of non-offspring can either be non-breeding or have dependent offspring on their own.

Despotic societies, in which only the dominant female breeds, and subordinates of both sexes help to rear her young, are often called “helper at the nest societies”. Mammalian examples of such societies include wild dogs (*Lycaon pictus*), golden and black-backed jackals (*Canis aureus*, *C. mesomelas*), dwarf mongooses (*Helogale parvula*), meerkats (*Suricata suricatta*) and naked mole-rats (*Heterocephalus glaber*). Groups in which most or all females breed and cooperate during the rearing of young, on the other hand, are often termed “communal breeder societies” (Fig. 1). Lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), coatis (*Nasua nasua*) and banded mongooses (*Mungos mungo*) are mammalian representatives of such societies. However, as noted above, these represent merely the extremes of a continuum, and the number of breeding and non-breeding females varies intra-specifically. In dwarf mongooses generally only the alpha pair produces a litter, and subordinates of both sexes help to raise the altricial young, which cannot move with the pack for 6 weeks; sometimes, however, subordinate females also become pregnant and nurse joint litters [19]. In house mice there are also social groups in which non-breeding female subordinates groom and carry the pups of a breeding female and others, in which only breeding females share a communal nest [20]. The evolutionary reasons why non-breeding females care for the young need not be identical to those of cooperation among breeding females. Therefore I suggest that to understand the phenomenon of communal care we should discriminate between the care provided by non-breeding group members and that provided by breeding females.



Fig. 1. A mammalian example for obligate cooperative care, the East-African naked mole-rat (*Heterocephalus glaber*). Non-breeding colony members of both sexes help the dominant female to rear her litters. (Drawing by Dafila Scott from [53], with kind permission)

Cooperative care of young by non-breeding group members

The offspring of a breeding female are also cared for by other, non-breeding individuals (of both sexes) in the group. Non-breeding helpers generally provide at least qualitatively the same parental behaviour as the mother (or the parents). Subordinate helpers groom, lick, carry and protect the young, keep them warm and bring food to the pups once they are old enough to eat solid food. Lactation by female non-breeders, however, is known from only few species, such as meerkats and dwarf mongooses, where 4% of the subordinates enter a cryptic pseudopregnancy, then lactate and nurse the dominant's young (T.H. Clutton-Brock, personal communication; [21]). Cooperative care of the young by non-breeding group mem-

bers has been described primarily for carnivores, rodents, primates and proboscideans (elephants). For many other social species with multi-female groups only little information is yet available on this behaviour (e.g. marsupials, chiropterans, cetaceans).

Cooperative care among breeding females

Females rear their own offspring and simultaneously provide care for the young of other group members. Such cooperative care of breeding females typically involves the same maternal behaviours as those above. In most of these cases breeding females nevertheless discriminate between their own and alien young and preferentially invest in their own offspring. This is especially obvious during nursing. Packer et al. [22] reviewed 100 species of mammals in 14 orders for the occurrence of allonursing. Non-offspring nursing was found more often in captivity than under natural conditions. According to field studies on 82 non-domesticated species, non-offspring nursing was absent or occurred only in the form of some milk stealing by young in 60% of the species, in 30% one's own offspring were nursed substantially longer or more often than alien ones, and in only 10% of the species were alien pups nursed as much as one's own young. In general, non-offspring nursing occurs in all major mammalian taxa and seems to have evolved independently under a variety of conditions [13].

Benefits and costs of group living

Before discussing the possible benefits of cooperative care of non-offspring for a breeding or non-breeding female we must first consider the evolutionary reasons why female mammals live in groups as a prerequisite for helping others to rear pups.

The two most prominent environmental factors that affect group living in all major animal taxa are food and predators (for a detailed description see [23]). In mammals the association with conspecifics can improve an individual's feeding success due to easier access to and better defendability of territories or good feeding sites due to improved information about where food is available or because of the possibility to catch large or elusive prey by cooperative hunting [24–27]. Group living can also improve protection against predators because of cooperative defence, increased vigilance (many eyes see predators better than a single pair of eyes), the dilution effect

(the probability of any given individual being taken during a successful attack by a predator decreases with increasing size of the group), and the confusion effect (evidence shows that predators are confused when attacking a dense group of prey and preferentially attack small groups or single individuals [28–30]). Furthermore, group living may be beneficial because of lowered metabolic costs, improved protection against unfavourable abiotic conditions [31–34] and better protection against ectoparasites due to allogrooming [35].

On the other hand, we know from many examples that an individual also suffers costs from living in a group, such as increased competition with group members over food, nest sites and mates [36–38], increased probability of infection with parasites and diseases [39, 40], greater conspicuousness to predators [41], and costs of vigilance [42, 43].

The fact that many mammals live in groups implies that here the benefits outweigh the costs [23, 44]. Nevertheless, the costs involved in group living may hinder or even prevent the evolution of social behaviour among group members, especially if a social or cooperative act involves any fitness costs in terms of reduced future reproduction for the acting individual. A behaviour that provides a benefit to its recipient at some cost to its performer is called altruistic [45]. In 1964 Hamilton [46] noted that relatedness can be of paramount importance in the evolution of such altruistic behaviour. He pointed out that an individual can maximize its fitness not only by direct reproduction but also indirectly by helping kin to produce and/or rear additional offspring (indirect fitness benefits). Depending on the degree of relatedness between the donor and the recipient of help, such offspring may carry copies identical by descent to the helping individual (for a detailed description see [23, 47]). According to this so-called kin selection mechanism [48], altruistic behaviour should be more common in groups of related individuals. Other mechanisms that may support the evolution of altruistic behaviour are mutualism (each partner gains fitness benefits by performing the altruistic behaviour) and reciprocity (as long as the altruistic act is reciprocated at some later date, both partners gain fitness benefits). Such mechanisms can explain altruism even among unrelated individuals, although it may evolve more easily in groups of relatives [49–51].

Is cooperative care of young altruistic?

Several of the above behaviours illustrating cooperative care can be costly in terms of its bearer's future

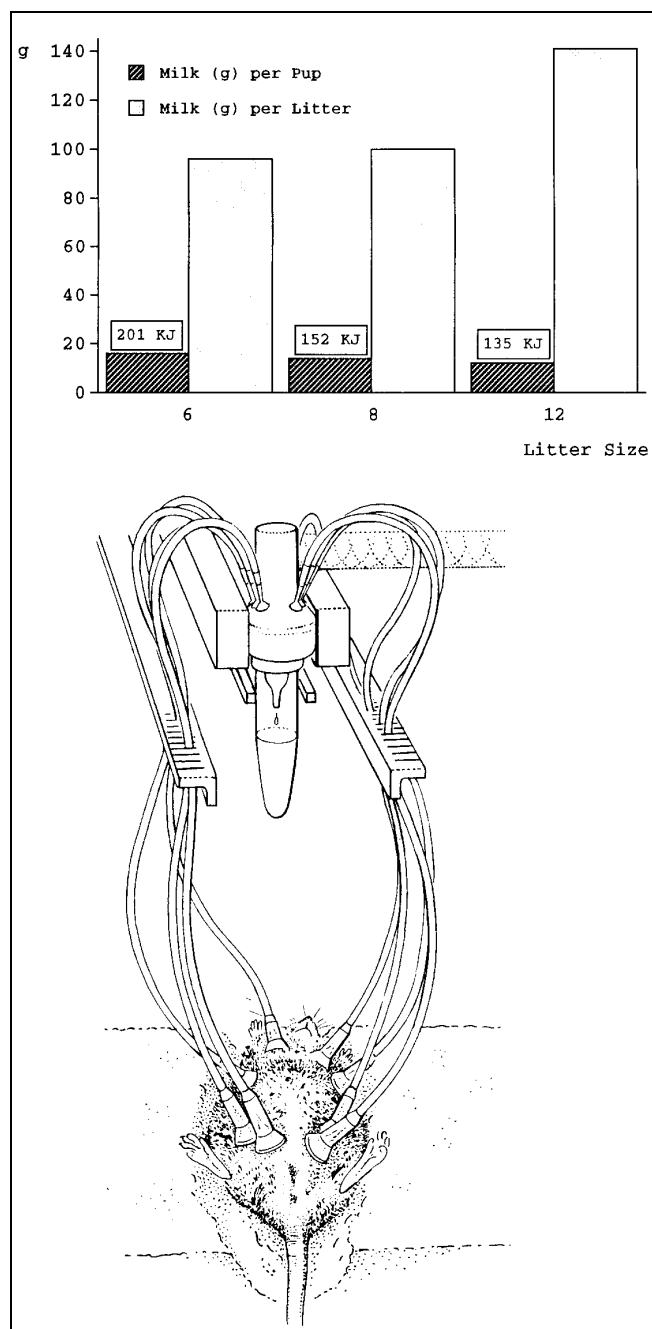


Fig. 2. Total amount of milk (g) provided by female house mice (*Mus domesticus*) rearing differently sized litters for individual pups and for the entire litter during a lactation period of 22 days. For pups the total energy equivalent of the milk provided is also given (in kJ; above columns). The amount and quality of milk were evaluated by milking mice with a special milking device. (Data from [55])

reproductive success. The most obvious candidate for altruism is certainly nursing [52, 53]. Broodcare in mammals is characterized by female lactation, which in most species is much more demanding in terms of energy than is gestation. The energy costs of lacta-

tion have been evaluated by analysing a mother's food consumption and milk production [53–56]. The amount of milk that a female produces is usually limited even under unlimited food availability and influences both the growth of the young and the mother's future reproductive success. In house mice, for example, a female, must produce approximately 100 ml milk, at an energy equivalent of 1100 kJ, over a period of 3 weeks to wean a litter of seven pups [55] (Fig. 2). The amount of milk that a pup receives determines its weaning weight, which affects the age of maturity and dominance status later in life [57]. Females increase the total amount of milk produced with increasing litter size. However, regulation is imperfect, and individual pups in very large litters receive less milk and are weaned at a lower weight than individuals in smaller litters [55, 58]. For the mother, on the other hand, increasing milk production entails reproductive costs because the more milk produced during lactation the more delayed is the birth of the next litter [57, 59]. As a consequence we should not expect females to provide milk to non-offspring which is no longer available to her own young.

Warning or defending pups against a predator can also be altruistic because it involves risking one's own life, with very negative consequences for the helper's future reproductive success. For other behaviours, such as babysitting, grooming, licking and playing with pups, the reproductive costs are difficult to assess and are often rather low. Nevertheless, such behaviours may involve at least opportunity costs if the helper could instead spend the time searching for food or otherwise improve its survival or future reproduction.

Thermoregulation in homiotherms involves relatively high energy costs, especially for young animals with an unfavourable surface-to-volume ratio. Growth and survival of offspring often depend on how efficiently they control their body temperature. Warming by adults can help young mammals to fulfil this goal. For the helper, on the other hand, keeping pups warm can be costly. In Alpine marmots (*Marmota marmota*), social thermoregulation among breeding and non-breeding adults reduces individual heat loss and energy consumption, which is reflected in lowered loss of body weight during hibernation. The presence of juveniles, however, increases the energy costs of non-breeding helpers during hibernation [60, 61].

Why do individuals care for non-offspring?

The care of non-offspring may not always be adaptive but rather be a kind of maldirected or mistaken parental care [7, 62, 63]. However, in the case of well-developed, regular alloparental behaviour we must assume that the helping individual gains either direct or indirect fitness benefits, despite the costs mentioned above. Indirect fitness benefits can accrue only if care of non-offspring is directed towards non-descendant kin. This option should be available often in social groups of mammals because they typically consist of extended family groups which form when offspring (mainly females) remain associated with their parents into adulthood [64] (the question of why such family groups evolve is discussed elsewhere [65, 66]).

Subordinate, non-breeding group members are constrained in their reproduction by both ecological and intra-group conflict factors [65, 67, 68]. Here we do not review the reasons why subordinate mammals lack the option to rear their own young, but we focus on the question of why they invest in non-offspring instead of using all available resources to improve their own growth and/or survival and increase their future probability to reproduce. From studies with cooperatively breeding birds we know of several direct benefits that can accrue to helpers which enhance a helper's probability to survive, its likelihood to become a breeder in the future, or its fecundity when it does become a breeder [69]. In mammals such direct benefits have been little studied, and they require either long-term field data of individuals performing various levels of non-offspring care or experimental manipulation of the number of non-breeding helpers. It has been hypothesized mainly for primates that experience in the care of young improves future success as a mother ("learning to mother" [70]), and that the care of non-offspring enhances the helper's status, especially if the infant's mother is of high rank [71].

There are more data available on the indirect benefits of cooperative care. Several studies suggest that the presence of non-breeding helpers increases the number of offspring raised in the group, as is the case in Alpine marmots, two species of jackals and pine voles [61, 72–74] (Fig. 3). In some species non-breeding helpers are in fact crucial to rearing young, as the parents alone are incapable of reproducing successfully, such as wild dogs, tamarins and dwarf mongooses [75, 76]. In most cases in which non-breeders care for non-offspring, such care is provided exclusively or preferentially to the young of close relatives, such as mother, daughter and sister. In addi-

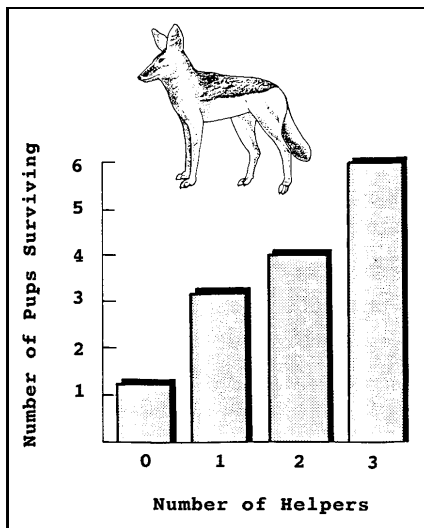


Fig. 3. Cooperative care of young in blackbacked jackels (*Canis mesomelas*). The number of offspring raised by the breeding pair increases with increasing number of non-breeding helpers. (Modified from [11]; data from [72])

tion to the species discussed above, this is the case in African and Asian elephants, naked mole-rats, and voles. In Alpine marmots, brown hyaenas and house mice the genetic relatedness has even been shown crucially to determine the degree of cooperation provided [61, 77, 78]. In most species, however, it remains to be shown that cooperative care by non-breeders actually increases the dominant breeder's fitness [14]. Under severe ecological constraints the care of non-descendant kin might result in a higher total fitness than would the option to leave and to try to reproduce alone.

Once several females breed within a group, the question arises as to why they should care for their young communally. This, again, is expected if breeding females gain direct benefits. For example, due to improved survival of their own young in the presence of other lactating females, allomothering may enable lactating females to increase food consumption and to enjoy other energy benefits. Offspring could further benefit by improved thermoregulation and/or growth, by the dilution effect, and by improved competition later in life (for recent reviews see [22, 79–81]). As noted above, indiscriminate communal nursing, the most prominent example of altruistic care of non-offspring, is rare among mammals. It can nevertheless improve a female's lifetime reproductive success. House mice (*Mus domesticus*) most typically live in small family groups that consist of a dominant male, one to several females with their litters and some subordinate animals of both sexes. Breeding females that belong to the same

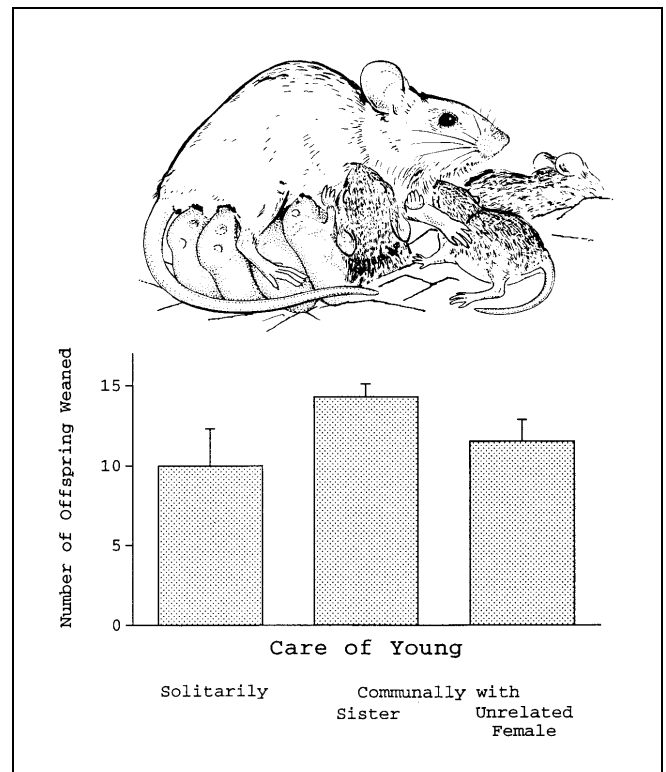


Fig. 4. Female house mice (*Mus domesticus*) that rear litters communally with a sister wean more offspring during their lifetime (under laboratory conditions) than females rearing litters alone or in the presence of a previously unfamiliar, genetically unrelated partner. Data are given as medians plus standard errors. (Data from [83])

group are often related and pool their litters in a communal nest, in which they indiscriminately nurse their own and alien young [82]. Under laboratory conditions, females that share a nest with a familiar sister had a higher lifetime reproductive success than females rearing litters alone [83]. This was due to a higher probability of reproducing and of improving the survival of offspring born by females sharing a nest with a sister. Here the phenotypically altruistic behaviour of nursing non-offspring proved to be genetically "selfish" by maximizing individual lifetime reproductive success in comparison to rearing litters alone or in the presence of a previously unfamiliar, unrelated female partner [20] (Fig. 4).

For many species no benefit from cooperative care by breeding females has yet been established. For example, in African elephants the suckling of calves by non-mothers is unlikely to enhance the nutritional intake of calves [84]. Non-offspring nursing by breeding females has also been thoroughly studied in lions, where it occurs mostly among close kin; however, females nevertheless prefer to nurse their own young. Here Pusey and Packer [85] detected no ben-

efit for either the females or the young and concluded that communal nursing is a by-product of female sociality. Females live in groups because of the benefit of communal defence of their cubs against infanticide, and the nursing of non-offspring is due to the low costs involved for a lactating female [85].

Another hypothesis, not yet tested in mammals, is that cooperative provisioning of young evolves by reciprocity when breeders provide their litters asynchronously under environmental conditions that threaten the survival of young due to starvation. Cooperative provisioning does not increase the main food intake of each offspring, but asynchronous communal provisioning would decrease the interval between meals and thus decrease the risk of starvation [86].

Non-offspring care is not necessarily restricted to relatives among breeding group members, such as in the case of Bolivian squirrel monkeys (*Saimiri b. boliviensis* [87]), evening bats (*Nycticeius humeralis* [80]), 13-lined ground squirrels (*Spermophilus tridecemlineatus* [88]) or house mice (*Mus domesticus* [83]). In general, however, the incidence of nursing alien young seems to be significantly correlated with relatedness among the females within social groups and with litter size. Under natural conditions non-offspring nursing is more common in species with large litters that live in small family groups. In species with single offspring (e.g. in many primates and ungulates) non-offspring nursing is rare and typically involves milk theft by parasitic young [22].

Why is non-offspring nursing so rare?

Although there is still a great need for molecular studies on the genetic relatedness between donors and recipients of help, cooperative care by non-breeding group members in mammals may best be explained by indirect fitness benefits in a situation in which the option of successful direct reproduction is not available. Nevertheless, it is striking that the care provided by non-breeders only rarely involves nursing. Why is lactation by subordinates so rare, while in birds feeding by non-breeding helpers is very common [7, 8]? According to Daly [89], a female's reproductive success is limited not by her lactational capacity but by food availability during the most arduous season of the year. However, it is difficult to believe that "assistance in lactation would not increase a female's reproductive capacity and the growth and survival of her progeny" [53]. No fundamental physiological constraints are known that

might prevent non-breeding individuals from producing milk. Spontaneous lactation, without prior pregnancy, has been documented for female dwarf mongooses, dogs and primates (including humans) and can be induced in laboratory rodents by repeated exposure to newborn pups (literature cited in [21]). Even in males lactation cannot be excluded in principle [89], and there is evidence of milk production by males in a population of Dayak fruit bats (*Dyacopterus spadiceus*) in Malaysia [90]. Furthermore, endocrine changes in males (heightened prolactin levels) have been postulated as a correlate of paternal behaviour in biparental species such as the California mouse (*Peromyscus californicus* [91]) and the common marmoset (*Callithrix jacchus* [92]). Jennions and Macdonald [14] speculate that "differences between birds and mammals in the possible forms of parental care (feeding in birds versus suckling in mammals) may be important in generating differences in the expression of cooperative breeding between these taxa."

A basic difference between birds and mammals may be the much higher costs of lactation than those of other types of parental care. The benefits of non-offspring nursing are probably seldom large enough to offset the costs for a non-breeder. Milk production typically requires increased food consumption and regular visits to the sucking young, which may increase a non-breeder's predation risk or mortality during unfavourable environmental conditions and/or interfere with a subordinate's body maintenance or growth. Another cost of non-offspring nursing may derive from the fact that lactation often suppresses further oestrous cycles (lactational anoestrus [93, 94]). As a consequence a lactating subordinate may be unable to respond quickly to reproductive opportunities that present themselves unpredictably. The absence of nursing in the majority of non-breeders may also be explained by a conflict of interest with the dominant breeder, who could risk losing reproductive control over the subordinate once it lactates. Subordinate dwarf mongooses that succeed in producing a litter had often been lactating spontaneously during the preceding season [21]. This illustrates the potential costs for a dominant breeder in allowing subordinate non-offspring nursing.

Although not widespread, non-offspring nursing is more common among breeding than non-breeding females. This could be due to more similar evolutionary interests among reproducing females and more symmetrical benefits and costs that facilitate the evolution of mutualistic or reciprocal cooperation. The probability that a non-breeding subordinate's help towards offspring of a breeding female will be reciprocated at some later time is certainly much lower than

the probability that two breeding females will both have another litter and share another communal nest.

Prospects

Quantitative analyses are still lacking for most mammals regarding the costs and benefits involved in non-offspring care provided by non-breeding versus breeding individuals. Such analyses are necessary to determine whether cooperative care is adaptive. We also need more information on the genetic relatedness among group members and the affect of this on the willingness to care for non-offspring. Furthermore, little is known about the way in which ecological conditions affect the willingness of subordinates to assist in the care of non-offspring. In wolves, for example, the availability of food influences the ability or willingness of pack members to provide food or other care for pups: when food is abundant, there is a positive correlation between pack size and litter size, but when food is scarce, pack size and litter size are negatively correlated [95]. These gaps in our knowledge and understanding of cooperative care of young in mammals will hopefully soon be filled with new and exciting results.

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