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Cooperative breeding in mammals

Michael D. Jennions and David W. Macdonald

Cooperative breeding in mammals covers a diversity of breeding systems. In all cases, however, individuals assist in the rearing of offspring other than their own. Recent research has highlighted some of the factors responsible for variation both within and between species. While it is possible to generalize about the selective pressures leading to cooperative breeding, doing so may obscure important contrasts between taxa. Of course, inclusive-fitness models explain the generalities of cooperative breeding, but differences in ecology, physiology and life history may result in distinctive processes operating in different taxa – data only likely to emerge from long-term field studies.

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Most studies of cooperative breeding in vertebrates have been on birds[1,2]. This has led to the development of a conceptual framework which is generally assumed to be applicable to mammals. While most of the experimental and correlational tests have also been on birds[2–4], new research on cooperative breeding in mammals provides an opportunity to investigate the generality of bird-based models.

What is cooperative breeding?

In the bird literature, cooperative breeding is defined as a situation where 'more than a pair of individuals exhibit parent-like [helping] behaviour towards young of a single nest or brood'[4]. In mammals, this type of behaviour has been recorded in numerous taxa, ranging from rodents to elephants[5,6]. Activities defined as 'helping' in mammals (see Box 1) include feeding, grooming, babysitting[7], helping infants in distress[8], assistance in thermoregulation[9] and allosuckling[10]. In practice, 'helping' has been used to describe any activity directed towards infants or their parents which is likely to benefit the recipients and increase breeding success (e.g. alarm calling or provisioning a pregnant female). By definition, then, all animals which are social during the breeding season are cooperative breeders. We suspect, however, that workers are most interested in a subset of costly helping behaviours – those which appear to decrease the donor's direct fitness relative to that it would possess if it did not perform these activities (Box 2).

Is 'helping' beneficial for breeders?

An important variable in cooperative-breeding models is the influence of helping on breeder fitness, and correlational evidence is often used to calculate the magnitude of this effect. Positive relationships between the number of helpers and reproductive success have been recorded for some mammals (Table 1), but others have failed to show this effect. However, relationships are potentially confounded by factors covarying with group size, like breeder experience or territory quality[3,11]. This problem can be addressed through experimental manipulation. In birds, by removing helpers, two studies have shown that helpers are beneficial, and a third that they have no discernible effect[11]. Experimental removals have been carried out on two mammals – prairie voles (*Microtus ochrogaster*) and pine voles (*Microtus pinetorum*)[12,13]. In both species, philopatric juveniles groom and brood young and assist in burrow maintenance. Statistically significant differences in some reproductive variables were recorded (Table 2). Although suggestive of increased life-time reproductive success for breeders with helpers, it remains to be shown that these effects translate into increased breeder fitness.

Further experimental removals may clarify the situation, but their results will need to be interpreted with caution. First, group-size effects may be responsible for the increased reproductive success of breeders in larger groups[11]. Many cooperatively breeding mammals are highly social,

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foraging in cohesive groups, and direct benefits from group size, such as improved foraging efficiency, could increase breeder reproductive success irrespective of helping that is specifically directed at infants or breeders. Similarly, increased breeder survivorship may arise due to improved predator detection in larger groups[14], rather than from a decreased parental burden due to directed helping. Second, removals are disruptive. Changes in social structure, especially in species with division of labour, might exaggerate the perceived benefits of helping. Anecdotal evidence suggests that even natural deaths can have strong effects on group stability and increase the level of aggression within groups. Removals should thus be performed well in advance of observations.

An alternative approach to the experimental removal of helpers is the use of multiple regressions where the affects of 'habitat quality' and 'breeder experience' are controlled for[15]. However, if increased numbers of helpers improve 'habitat quality' (due to territory expansion or shifts), the benefit from their presence will be underestimated. Another approach is to regress changes in group reproductive success on natural changes in group size (through mortality and migration) (S.R. Creel and P.M. Waser, pers. commun.). Both approaches have shown a significant effect of group size on reproductive success in dwarf mongoose (*Helogale parvula*)[15].

Causes of delayed dispersal

In most species, cooperative breeding arises due to delayed dispersal from natal territories. There has been much debate in the ornithological literature as to whether 'ecological constraints' (such as saturated habitat, absence of mates or a low probability of successful dispersal) or 'benefits of philopatry' cause delayed dispersal[3,4]. However, the emerging consensus, encapsulated by the 'delayed-dispersal threshold' model, is that no single factor causes delayed dispersal and cooperative breeding. Instead, fitness differences between floaters, delayed dispersers and early dispersers that attempt to breed are related to population density, mate availability, the effects of helping, the distribution of territory quality and spatio-temporal environmental variability[3,4]. The challenge is to determine the relative importance of these factors in different species by measuring costs and benefits associated with different strategies: costs which select for delayed dispersal, and benefits which select for helping.

Studies in birds clearly show that territory quality influences dispersal decisions[3,4]. At the simplest level, delayed dispersal occurs when there is an absence of territories that can support a breeding pair. Experimental manipulation of territory availability in birds has shown that potential helpers are more likely to disperse and attempt to breed when suitable territories are vacant[16]. Similar experiments with white-footed mice (*Peromyscus leucopus*)[17] show that communal breeding, due to retention of daughters on natal territories, decreases when vacant territories are made available (J. Wolff, pers. commun.). In dwarf mongooses[18] and European badgers (*Meles meles*)[19], territories sometimes remain unoccupied. However, in the former species, these territories often have a history of low productivity (S.R. Creel, pers. commun.), suggesting that the benefits of philopatry, through inclusive fitness gains, outweigh any direct fitness gains likely to arise from attempting to breed on a 'vacant' territory. There is also evidence that individuals do not simply classify territories into 'suitable' and 'unsuitable', but make more fine-scaled distinctions[16]. In mammals, little fieldwork, but much theorizing, has investigated the effect of variation in territory quality on individual dispersal decisions and experimental manipulation of territory quality is likely to be a profitable line of future research.

What benefits accrue to helpers?

Given the above 'constraints' on dispersal, what benefits tip the balance in favour of delayed dispersal? Two benefits of remaining at home in a group are widely recognized – reduced predation risk and improved foraging efficiency[20]. The third set of benefits is accrued through helping. Emlen and Wrege[21] reviewed nine benefits to being a helper in birds, and most of these seem to have mammalian counterparts (Table 3). In addition, there are also some novel hypotheses that have not been used to explain helping in birds. For example, in evening bats (*Nycticeius humeralis*), females may derive a direct benefit from allosuckling by reducing the weight of the milk load prior to foraging[22]. Non-adaptive explanations for helping have been proposed for birds, but they have received little support on the grounds of implausibility (maladaptive behaviour will be selected against) and confusing levels of analysis (not distinguishing between the historic origins of a behaviour and its current function)[23]. In mammals, however, some behaviours defined as helping do not appear to benefit the donor. Thus, they might be tentatively labelled as functionally maladaptive: for example,

misdirected parental care in seals[24] and allowing 'parasitism' through milk theft[5] (but see below).

Historically, a major preoccupation has been the extent to which indirect selection contributes towards the inclusive fitness gains from helping[1-3]. Two bird studies have concluded that indirect selection is essential for the maintenance of helping[23,25]. Evidence that indirect selection has shaped helping behaviour in mammals comes from studies where the relatedness of helpers to young affects the amount of help provided. In brown hyaena (Hyaena brunnea), provisioning rates are higher when helpers are more closely related to young[26]. In alpine marmots (Marmota marmota), subordinates overwintering with breeders generate heat to assist in thermoregulation, thereby losing body weight. Subordinates lose more body weight when hibernating with juveniles that are potential full sibs than with less-closely related juveniles, suggesting a role for indirect selection[9]. However, the absence of fine-tuned adjustment of levels of helping in proportion to relatedness does not invalidate a role for indirect selection. Helpers may use simple 'rules of thumb', only helping when their expected relatedness to young exceeds a threshold value. This may lead to occasional 'mistakes' when the actual degree of relatedness falls below the mean expected value. These 'mistakes' may also account for behaviour such as misdirected parental care.

Ironically, helping may sometimes evolve to the extent where it also becomes a constraint. In species like wild dog (Lycaon pictus), dwarf mongoose and tamarins (Saguinus spp.), the energetic costs of breeding may be so high that a lone pair is effectively incapable of reproducing successfully[27]. The costs of reproduction in these species have probably risen in response to the increased workforce available[4,27]. Helpers thus become a necessary resource which constrains dispersal in the same way that absence of a mate would. A recent comparative study of birds has shown that cooperative breeding is non-randomly distributed between lineages, although the reasons for this remain obscure[28]. In mammals, once the costs of reproduction have increased to the extent that cooperative breeding is obligatory, they may also act as a phylogenetic constraint, explaining the frequent occurrence of delayed dispersal and cooperative breeding within certain lineages (e.g. canids or tamarins).

Breeding by subordinate females

Attempts to breed in their natal group provide another route by which subordinates can benefit from delayed dispersal. The potential for successful pregnancy in subordinate females illustrates a possible case of phylogenetic constraints. In birds, intraspecific clutch parasitism may go undetected, and female helpers might be able to add eggs to clutches[29]. In scrub jays (Aphelocoma coerulescens), breeders often keep helpers away from the nest until egg laying is completed[11]. However, DNA fingerprinting of stripe-backed wrens (Campylo rhynchus) did not reveal breeding by subordinate female helpers[30]. Even so, the causes and frequency of subordinate pregnancies might differ dramatically between birds and mammals. In birds, subordinate females will generally benefit from adding eggs to clutches (assuming that the cost of egg production is relatively low when compared with the risk of detection). In mammals, by contrast, pregnancy by subordinates is undoubtedly expensive because of the high costs of gestation[27] and the ease of detection by dominants. We might thus expect subordinate mammals to conceive only when the dominant pair, or other group members, are likely to tolerate the subordinate's offspring.

Table 1. Correlational evidence[a] for an effect of helpers[b] on breeder fitness

Species	Correlation	P	Refs
Dwarf mongoose (Helogale parvula)	0.53	<0.001	18
Lion (Panthera leo)	–	<0.01[c]	10
Silverbacked jackal (Canis mesomelas)	0.89	<0.01	46
Golden jackal (Canis aureus)	0.36	<0.05	46
African wild dog (Lycaon pictus)	0.85[d]	0.06	35
Coyotes (Canis latrans)	Positive	NS[e]	47

[a]The correlation is usually between the number of helpers (or group size) and the number of infants surviving to a biologically meaningful age, such as mean age at weaning.
[b]Breeders that allosuckle other females' infants are also classified as helpers (e.g. lion).
[c]Based on an ANOVA of per capita reproductive success. Medium size groups had the highest success, suggesting an upper limit, beyond which the effects of 'helping' are outweighed by other factors.
[d]Excluding litters where no offspring survived.
[e]NS, not significant.

Recent work on dwarf mongooses has provided detailed empirical data on the circumstances under which subordinates conceive[31]. This supports an inclusive-fitness model for subordinates suggesting that they facultatively adjust their likelihood of producing offspring to maximize inclusive fitness. They are more likely to become pregnant when the benefits of staying in a group and helping are less than those gained from dispersing and attempting to breed. The most important proximate factors responsible for this shift in benefits are that the indirect benefits of helping declined as females age and relatedness to the breeders decrease, while the likelihood of dispersing and breeding successfully increases with female age owing to greater dominance. As predicted by the model, there were more subordinate pregnancies in older females. As helping became less beneficial for subordinate females, additional 'incentives' seemed to be required to induce them to remain in the group[32]. Although theoretical work has focused on the size of these incentives[33,34], data on the extent to which subordinate reproduction affects the dominant's reproductive success are needed[31]. In dwarf mongooses, for example, if the dominant female could choose which subordinates bred, she would probably pick the younger ones because they are more closely related to her. However, it is the older subordinates that breed.

Interspecific studies have also addressed variation in reproductive suppression. In a comparative study using

Table 2. Experimental manipulation of the number of helpers under semi-natural conditions

Species	Effects of more helpers	P[a]	Refs
Prairie vole (Microtus ochrogaster)	Shorter inter-litter intervals.	<0.0001	12
	Infants spend less time alone.	<0.009	
	Frequency of pup grooming.	<0.05	
Pine vole (Microtus pinetorum)	Shorter inter-litter intervals.	< 0.005	13
	Larger weight at weaning.	0.008	
	Faster development.	0.05	

[a]Probability values are for ANOVAs. In some cases, each size is treated as a class, in others there are threshold effects and some size classes are lumped (e.g. 0–2 versus 3).

Table 3. Hypotheses to explain helping (with mammalian examples)[a]

Benefit to helper due to increased:	Proposed mechanism[b]	Mammalian examples	Refs
Survivorship	Group size improves vigilance, anti-predator behaviour or feeding success.	In evening bats (*Nycticeius humeralis*), females allosuckle unrelated pups (predominantly females), increasing colony size and future access to information about feeding sites.	22
	Helping is 'payment' for access to the natal territory.	In naked mole-rats (*Heterocephalus glaber*), there is conflict between the queen and workers over the amount of work performed, suggesting that some 'payment' is extracted (although conflict may occur for other reasons as well).	44,45
Future probability of territory holding	Larger groups expand their territories.	Naked mole-rat colonies probably divide by fission. The likelihood that the daughter colonies will succeed is probably related to size of the workforce.	44
Future probability of breeding	Helping results in coalitions between donors and recipients, and coalitions are more likely to acquire vacant territories than are lone individuals.	In dwarf mongooses (*Helogale parvula*), recipients and donors of help may disperse together. In lions (*Panthera leo*), mothers increase the likelihood of their offspring obtaining coalition partners by allosuckling. Larger coalitions are more successful (but also tend to comprise closely related males due to the increased skew in mating success).	10,18,39
	Helpers form bonds with opposite-sex breeders and are more likely to be chosen as future mates than non-helpers.	Little or no evidence for this in mammals, although Rasa has suggested that in dwarf mongooses, males that help more are more likely to be future breeders.	48
Reproductive success	Helpers gain breeding experience, which increases their own breeding success.	In many mammals, more experienced individuals have increased success in raising young. However, it remains to be shown that helpers are more successful than non-helpers when they first breed.	
	Helpers are more likely to gain the support of recipients of help as future helpers.	In dwarf mongooses, many helpers eventually breed in their natal group. Given that delayed dispersal is common, helpers will thus gain a future direct benefit. However, it remains to be shown that this benefit is greater than the initial cost of helping which requires a comparison between helpers and non-helpers.	18,31
Production of non-descendent kin	Increased survival of related breeders, hence higher reproductive success for breeders.	Breeders have higher survivorship when helpers are present in dwarf mongooses and lions.	10,18
	Increased survival of recipients of help which are related to the helper.	In most cooperatively breeding mammals, helpers and donors are closely related and substantial indirect benefits may be realized.	2,3,37,39

[a]See Ref. 3.
[b]Larger group size is assumed to be a consequence of helping.

generic means, it was found that suppression in Carnivora is associated with increased energetic costs to reproduction. Gestation costs (litter size and mass) and postnatal investment (litter growth rate and total energy invested) are higher in cooperative breeders with reproductive suppression than in those without[27]. A more robust comparative analysis using Alan Grafen's phylogenetic regression has confirmed this trend (S.R. Creel and D.W. Macdonald, pers. commun.). Subordinates seem to be more likely to forgo reproduction when the cost of a breeding attempt is high. In mammals, various degrees of reproductive suppression are found – ranging from nearly complete suppression (e.g. wild dog)[35], to suppression of only a few group members (e.g. banded mongoose, *Mungos mungo*)[15], to no suppression (e.g. lion, *Panthera leo*, feral cat, *Felis domesticus*)[36]. As with allometric studies of morphology, it remains to be seen whether correlates of variation in suppression within species (e.g. group size) will also account for differences in the level of suppression between species. Those species that are predominantly plural breeders, but show interpopulation variation in the extent of suppression, like badgers[19], merit particular attention.

In dwarf mongoose, there is an additional twist to the saga: females may use pseudopregnancy as an adaptive strategy[37]. When a spontaneous lactator was present in a group, litter survival increased relative to that when only the dominant female lactated. Spontaneous lactators increased their inclusive fitness by 0.79 offspring equivalents. In contrast, in Ethiopian wolves (*Canis simensis*), litter size was significantly smaller when a subordinate female lactated. In the latter case, interpretation is complicated though, because allosuckling may have followed infanticide of the subordinate's litter by the dominant female (C. Sillero-Zubiri and D. Gottelli, pers. commun.).

Sneaky matings by male subordinates

In birds, studies have shown that male helpers sometimes successfully father offspring[30]. Fewer studies have been done for mammals, although in dwarf mongoose up to 25% of offspring are fathered by male helpers[38]. Shared paternity may be a substantial hidden benefit for helpers and its presence alters the predictions of models of male dispersal. More empirical data are needed on the extent to which helpers gain paternity in groups of different sizes, and whether the probability of mating is age or size dependent. DNA fingerprinting studies are likely to become de rigeur, as is already the case in ornithological studies. A recent study of lion illustrates the unreliability of

behavioural estimates of paternity[39]. DNA fingerprinting revealed an increased skew in male reproductive success in larger male coalitions, which was totally unexpected on the basis of behavioural observations.

Inbreeding and outbreeding

Mating by subordinates raises the issue of inbreeding. Theory suggests that close inbreeding will reduce offspring fitness, although no evidence for inbreeding depression was found in a recent and comprehensive field study of blacktailed prairie dogs (*Cynomys ludovicianus*)[40]. In cooperative breeders, the opportunity for parent-offspring matings is particularly high, but mechanisms appear to exist to reduce its occurrence. In birds and mammals, the main mechanism seems to be incest avoidance, and experimental evidence from white-footed mice suggests that reproductive suppression of non-dispersing juveniles is related to inbreeding avoidance rather than resource competition[17]. The cooperatively breeding splendid fairy wrens (*Malurus splendens*) show another solution, seemingly unique in birds but also found in several mammals. In splendid fairy wrens, more than 65% of offspring are fathered by males outside the group through extra-pair copulations[41]. Similarly, in Ethiopian wolves, there is almost no dispersal between groups. Dominant females mate with males from neighbouring groups indiscriminately but within the group they mate with only the dominant male, and even then this is at a lower rate than with neighbours (C. Sillero-Zubiri and D. Gottelli, pers. commun.). In brown hyaena, the only matings observed were with roving males[42]. In badgers, where dispersal may be very low, litters may contain offspring fathered by males outside the group[43]. In contrast, naked mole-rats (*Heterocephalus glaber*) appear to be highly inbred[44] and in alpine marmots, DNA fingerprinting and allozyme studies also suggest high levels of inbreeding[9]. A comparative analysis of rates of inbreeding in cooperative and non-cooperative breeders and its association with mating patterns remains to be done.

Conclusions

In birds as well as mammals, the evidence indicates that decisions either to delay dispersal and help, or disperse and attempt to breed, are based on the maximization of inclusive fitness which is influenced by the benefits of philopatry and the costs of dispersal. Surprising? Not really, but then again, much debate has surrounded the false dichotomies of costs or benefits, and indirect or individual selection. In reality, kin selection for direct and indirect fitness gains determines which is the best strategy; but in each species, the importance of each benefit and cost differs and must be determined empirically. The advantages of a large, thoughtfully collected data set are illustrated by the superb work on dwarf mongoose[15,27,31,37]. Elegant experiments on mammals have also yielded important insights[17,45]. Although we can only speculate at present, we think that differences between birds and mammals in the possible forms of parental care (feeding in birds versus suckling in mammals) and sex biases in parental care (biparental in birds versus lone females in mammals) may be important in generating differences in the expression of cooperative breeding between these taxa. As data accumulate, we suspect that the proximate causes of cooperative breeding, at least in terms of the relative importance of different factors, may also be shown to differ widely between lineages, but showing consistency within them (see also Ref. 28).

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