

The Evolution and Ecology of Cooperative Breeding in Vertebrates

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Cooperative breeding – in which some adults forgo independent breeding and remain as subordinates within a group helping to raise the offspring of others – occurs in between 3% and 10% of vertebrates. The structure of such systems varies greatly, from pairs with helpers-at-the-nest to communal breeders, and may include young helpers or post-reproductive ‘grandparents’. That some individuals spend part, or all, of their lives helping others to reproduce contradicts the concept of ‘selfish’ natural selection and provides an intriguing evolutionary paradox. When and why such apparently altruistic behaviour occurs has, therefore, been the focus of much study. Although constraints and the benefits of group living, may persuade individuals to remain as subordinates, indirect ‘kin’ benefits or direct benefits (such as becoming a breeding helper) appear to favour the subsequent evolution of helping. Cooperative behaviour can have wide-ranging consequences, not only on the biology of the cooperative species, but also on those species it interacts with.

Introduction

Evolutionary theory states that individuals are selected for their ability to efficiently translate resources into survival and reproductive success, maximizing their genetic contribution to future generations (Hamilton, 1964; Maynard Smith, 1964). This would appear to lead to a world dominated by selfish behaviour. However, the vast majority of animals live within a social environment, their lives affected by the presence and activity of others around them. They spend time interacting with others of their own, or other, species, they attract mates, care for offspring and group together for hunting or safety. Behaviour that provides a

benefit to another individual and, importantly, has evolved at least partly because of this benefit, can be defined as cooperative. Such behaviours pose a problem to evolutionary theory because they appear to reduce the relative fitness of the performer and hence should be selected against (Hamilton, 1964). As cooperation is apparent throughout the natural world there must be a solution to this paradox. However, while many instances of apparent cooperation are, after detailed investigation, explicable as the selfish motives of individuals, other forms of cooperation have proved more difficult to explain. For example, in some species individuals live and breed in bisexual groups of three or more adults and share in providing parental care at a single breeding attempt (Brown, 1987). Some of these adults are mature individuals that do not breed independently but instead care for young that are not their own genetic offspring. Typically, such cooperative breeding systems comprise family groups – e.g. a breeding pair and their offspring – that live together on permanent, stable, all-purpose territories. However, cooperative breeding systems may also comprise of individuals that help unrelated dominants to raise offspring (Koenig and Dickinson, 2004). Although in most species cooperative breeding groups contain only a small number of helpers, in several

Advanced article

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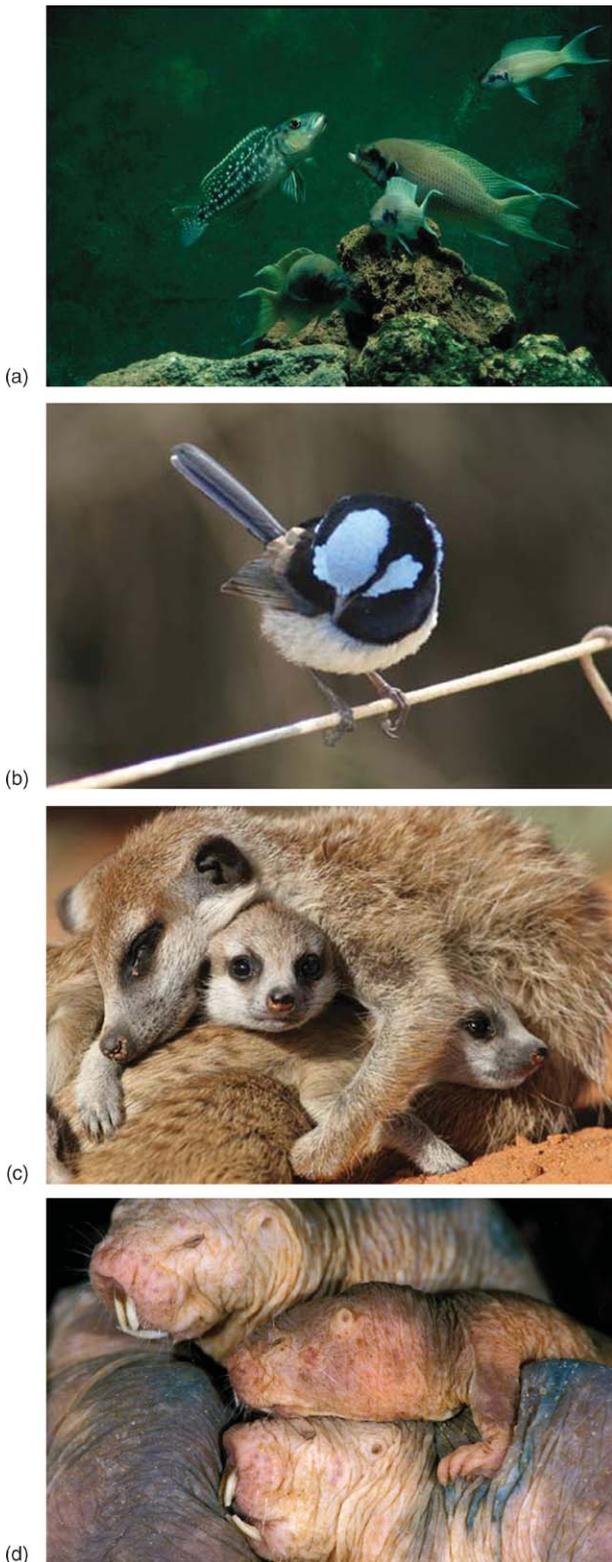
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species they may contain dozens, or even, as in the naked mole rat (*Heterocephalus glaber*), hundreds of helpers (Figure 1). Among vertebrates, cooperative breeding is found in at least 9% of birds, 3% of mammals and in some fish species.

In the last few decades, detailed long-term studies, which use modern molecular techniques to accurately determine genetic relationships, have revealed the true diversity and complexity of cooperative breeding. Systems may include a breeding pair assisted by nonbreeding helpers, as in the grey wolf (*Canis lupus*) and the naked mole rat. Alternatively a dominant pair may be accompanied by subordinates, of one or both sexes, that share reproduction with the dominant of the opposite sex (Figure 2). More recently, it has also become apparent that subordinates in cooperative breeding system may not always be young individuals yet to find an opportunity to breed independently, but may sometimes be older individuals that have stepped (or been pushed) aside to become subordinate helpers. Though this has been observed in only a very small number of mammalian species, e.g. pilot whales (*Globicephala macro-rhynchus*), baboons (*Papio anubis*) and humans, and in just one bird species, the Seychelles warbler (*Acrocephalus sechellensis*). Whatever the structure of the system, the fact that some individuals may spend part, or all, (i.e. naked mole rats) of their lives helping others to reproduce provides an intriguing evolutionary paradox.

The aim of this review is to discuss the evolution of cooperative breeding in vertebrates and to investigate how ecological and environmental factors may lead to such behaviour. We discuss cooperative breeding behaviour in relation to habitat use and quality, indirect and direct fitness benefits; resource competition and social interactions; social behaviour and population dynamics and inter-specific interactions. Throughout, we use the term 'subordinates' for mature individuals that cohabit with the dominant breeding pair either as nonhelpers, nonreproducing helpers or breeding helpers.

Theoretical Explanations for the Evolution of Cooperative Breeding

The classical theoretical framework for the evolution of cooperative breeding came from Hamilton (1964) and Maynard Smith (1964) who developed the theory now referred to as 'kin selection'. These authors argued that the fitness of each individual is determined by the total number of genes, identical by descent to its own, that are present in subsequent generations. Consequently, nonbreeding

Figure 1 Three species used in studies investigating the evolution of cooperative breeding in vertebrates: (a) Lake Tanganyika cichlid (*Neolamprologus pulcher*). A breeding group defending their territory against a predatory fish (photo: M. Taborsky); (b) superb fairy-wren (*Malurus cyaneus*). A dominant male (photo: A. Russell); (c) meerkat (*Suricata suricatta*). Subordinates help babysit the dominant pairs' offspring (photo: A.J. Young); (d) naked mole-rat (*Heterocephalus glaber*, photo: R. A. Mendez).

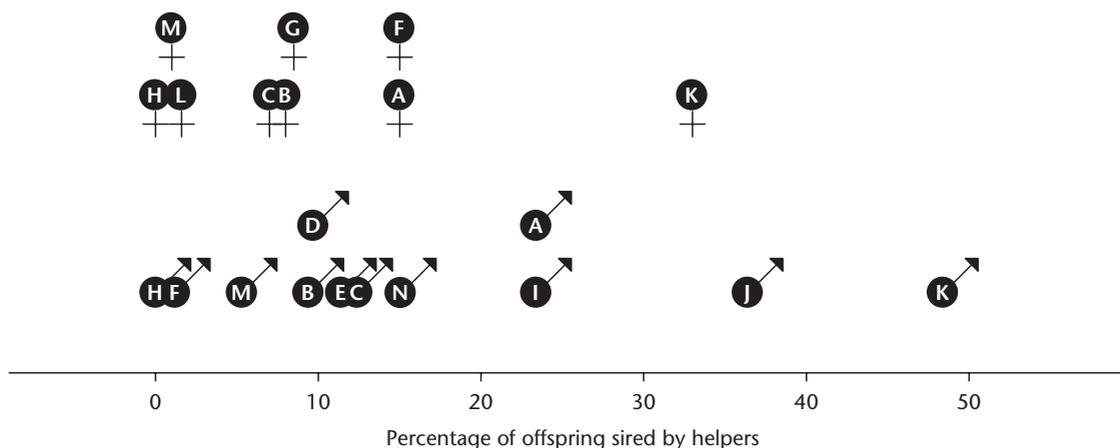


Figure 2 The percentage of group offspring that is sired by male and female helpers within populations of cooperatively breeding species. Although in some species helpers refrain (almost) completely from direct reproduction, in other species they produce nearly as many offspring as the dominants in the group. Furthermore, in some species helpers of one sex produce a considerably larger part of group offspring through direct reproduction than the other sex. In all cases parentage was assigned using molecular analyses. Species and sources: A, dwarf mongoose (*Helogale parvula*, Keane *et al.*, 1994); B, wild dog (*Lycaon pictus*, Girman *et al.*, 1997); C, meerkat (*Suricata suricatta*, Griffin *et al.*, 2003); D, Lake Tanganyika cichlid (*Neolamprologus pulcher*, Dierkes *et al.*, 1999); E, Lake Tanganyika cichlid (*Julidochromis ornatus*, Awata *et al.*, 2005); F, Seychelles warbler (*Acrocephalus sechellensis*, Richardson *et al.*, 2001); G, moorhen (*Gallinula chloropus*, McRae, 1996); H, Florida scrub-jay (*Aphelocoma coerulescens*, Quinn *et al.*, 1999); I, white-browed scrubwren (*Sericornis frontalis*, Whittingham *et al.*, 1997); J, Alpine accentor (*Prunella collaris*, Hartley *et al.*, 1995); K, pukeko (*Porphyrio porphyrio melanotus*, Lambert *et al.*, 1994); L, white-throated magpie-jay (*Calocitta formosa*, Berg, 2005); M, long-tailed tit (*Aegithalos caudatus*, Hatchwell *et al.*, 2002); N, superb fairy-wren (*Malurus cyaneus*, Double and Cockburn, 2003).

subordinates can increase their fitness indirectly by enhancing the reproductive success of close relatives (who carry the same genes). However, in most species the indirect genetic fitness benefit gained from helping is likely to be considerably less than the potential direct genetic gain from immediate independent breeding (Brown, 1987). Indeed, in some systems where subordinates are unrelated to the dominant breeders such indirect benefits are not possible at all. Therefore, understanding why mature individuals do not, or cannot, breed independently is the key to understanding the evolution of cooperative breeding. As such, the evolution of vertebrate cooperative breeding systems can be viewed as a two-step process; first, the decision by mature individuals to join a group and forgo independent breeding, and second, the decision, by subordinates in a group, to become helpers (Emlen, 1982). The first step is usually attributed to the existence of ecological or life-history constraints on independent breeding (Emlen, 1982). The second step envisages that individuals which become helpers within a group must gain a net fitness benefit through helping (Emlen, 1982).

Effects of Habitat Use and Quality

One important hypothesis argues that individuals become group members because ecological constraints, such as a lack of breeding opportunities due to habitat saturation (Selander, 1964) limit their ability to breed independently. This hypothesis was further developed by Emlen (1982) who suggested that joining a group should be favoured not only when mates and/or territories are in short supply, but

also when dispersal costs are high, or when the available breeding opportunities are relatively of poor quality. Individuals can only be expected to join a group if the benefits they receive – due to increased survival or increased reproductive benefits, be they indirect or in the future – exceed the benefits they would receive if they were not in the group. A critical prediction of Emlen's hypothesis is that subordinates are making the best of a bad job and would become breeders elsewhere if given a good enough chance. This 'ecological constraint' hypothesis was later refined by Stacey and Ligon (1987, 1991), who added a new perspective on the importance of variation in habitat quality for the evolution of cooperative breeding. The 'benefits of philopatry' hypothesis they put forward predicts that young will remain in groups on high-quality territories because the benefits they gain by doing so, in terms of direct benefits, such as increased survivorship, and indirect benefits due to helping, exceed the fitness they could gain by dispersing to breed independently on available low-quality territories.

Evidence that a shortage of breeding opportunities does indeed facilitate cooperative breeding has been provided by several studies. For example, in the Seychelles warbler the number of territories with subordinates increased as the habitat became saturated. The Seychelles warbler is a formerly endangered species whose range is restricted to a few small Seychelles islands. By 1940, anthropogenic disturbance had pushed this species to the verge of extinction and less than 29 individuals remained on the island of Cousin. In 1968, when the population consisted of just 26 individuals, habitat restoration programmes were implemented. Over the following 30 years, the population grew

impressively. No cooperative breeding was reported among Seychelles warblers until 1973, roughly the time at which all suitable breeding habitat became occupied (Komdeur, 1992). In essence, cooperatively breeding families formed when acceptable breeding opportunities first became constrained. In subsequent years, the population of mature birds has consistently exceeded the number of occupied territories. Interestingly, Seychelles warblers delayed dispersal and stayed in their natal territories as the habitat became saturated with territories. However, cooperative breeding did occur well before the island was completely saturated (Figure 3), suggesting that factors other than saturation also influence cooperative breeding.

To enhance the numbers of this endangered species, birds were introduced onto three nearby, previously unoccupied islands. To obtain birds for these transfers, breeding adults were removed from occupied territories on the original island. By this it was possible to create breeding opportunities. In the Seychelles warbler, removal of a breeder from a territory resulted in subordinates of the same sex rapidly moving in from other groups to fill the breeding opportunity. Breeder removal experiments were also conducted in the acorn woodpecker (*Melanerpes formicivorus*), the red-cockaded woodpecker (*Picoides borealis*) and the superb fairy-wren, and also in these species subordinates from other territories rapidly filled the breeding opportunity.

The simultaneous importance of both habitat saturation and habitat quality on subordinate dispersal was first provided by studies on the acorn woodpecker and the Seychelles warbler in the early 1990s. In these species the benefits, in terms of breeding success and survival, of remaining and helping on high-quality territories outweigh the benefits of independent breeding on lower-quality territories. Consequently, offspring from high-quality

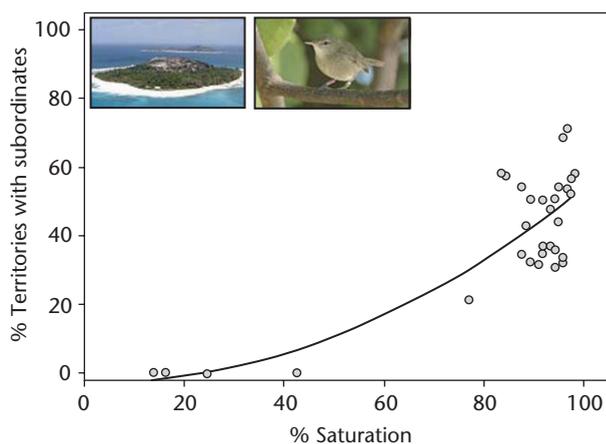


Figure 3 The percentage of territories with subordinates in relation to habitat saturation in a given year for the Seychelles warblers on Cousin Island between 1959 and 2006 ($r^2 = 0.67$, $F = 28.3$, $P < 0.001$). The percentage of habitat saturation for a given year was measured as the number of territories present in that year divided by the maximum number of territories recorded in a given year ($n = 121$). Island photograph courtesy of Lyanne Brouwer and bird photograph courtesy of Cas Eikenaar.

territories rarely disperse to fill vacancies in lower-quality areas. In the Seychelles warbler, the translocations of individuals to new unoccupied islands allowed this result to be experimentally verified. Initially all translocated individuals bred as independent pairs, but after all the good-quality territories were taken individuals chose to help on high-quality territories rather than to breed independently on lower-quality territories. Furthermore, in the original population vacancies created by the translocation of breeders were filled only by helpers from territories of equivalent or poorer quality, never by helpers from superior territories for which helping remained a better option than breeding. These results confirm that the 'benefits of philopatry' hypothesis can be accommodated within the 'ecological constraints' hypothesis by recognizing that these hypotheses differ only in the emphasis they place on either the costs of leaving or the benefits of staying (Komdeur, 2003). This realization has resulted in a more inclusive approach to investigating the evolution of cooperation, with emphasis on individual fitness-based decisions. An approach that has accounted for most of the progress towards understanding cooperative breeding systems in the last decades.

Indirect and Direct Fitness Benefits

Kin selection theory states that individuals are only expected to behave altruistically if the fitness benefits they gain via their relatives are greater than the costs of such behaviour (Hamilton, 1964; Maynard Smith, 1964). Social actions are ones that increase or decrease the offspring production of conspecifics. Hamilton (1964) realized that their evolution would be affected by relatedness. In other words, alloparental care will be favoured by selection only if $rb - c > 0$, where r is the genetic relatedness between the helper and the offspring helped, b is the fitness benefit to the offspring helped and c is the fitness cost of helping (Hamilton, 1964). Hamilton's rule therefore predicts greater levels of cooperation when the benefits (b) or relatedness (r) are higher, and lower levels when the costs of behaving in such a manner are higher.

So it is clear that a degree of relatedness between the helpers and the helped is essential if indirect benefits are to be accrued. High relatedness between interacting individuals within groups can be a result of active kin discrimination – where an individual distinguishes relatives from nonrelatives and preferentially helps relatives – or merely a consequence of limited dispersal (see later). Active kin discrimination has been demonstrated in several cooperatively breeding vertebrates, such as long-tailed tits (*Aegithalos caudatus*). In this species mature individuals try to breed independently, but if their broods fail they preferentially select nests of close kin at which to help raise offspring. The ability to recognize kin appears to be based on specific calls that offspring learn from adults while in the nest.

The widespread observation that cooperation routinely occurs among close relatives, especially in eusocial insects

where the haplodiploid sex-determination system means that females are more closely related to their sisters than to their own offspring, led to the early acceptance of kin selection as being key to the evolution of cooperative breeding (Koenig and Dickinson, 2004). However, the case for kin selection is not as strong as once considered, especially for vertebrates (Clutton-Brock, 2002). First, although most social vertebrate groups consist of relatives, it is not clear that relatedness is consistently higher in cooperative breeders than in species that live in stable, but non-cooperative, groups (Clutton-Brock, 2002). Second, in many systems the amount of help given does not vary with the relatedness of the subordinates and in some systems totally unrelated helpers often occur within groups (reviewed in Stacey and Koenig, 1990). Third, the magnitude of indirect fitness benefits relative to direct fitness benefits may have been over-estimated due to factors such as a failure to recognize the costs of competing with kin, the confounding effect of individual or territory quality, or an under-estimation of the extent of co-breeding by subordinates. Finally, extra-group paternity (with young sired by males from outside the group) occurs in many cooperative systems (e.g. Richardson *et al.*, 2001; Koenig and Dickinson, 2004). This complicates our understanding of cooperative breeding as extra-group parentage will reduce relatedness between subordinates and the offspring they help to raise and, consequently, the potential indirect benefits of helping.

Clearly then the evolution of cooperation does not always, or only, depend upon indirect fitness benefits; co-operation can also provide direct fitness benefits. For example, helping may lead to an increase in overall group size which, because larger groups are better at competing with other groups or deterring predators (Brown, 1987), increases the survival of all group members, including the subordinates. Such group augmentation does not require kinship within cooperative groups. Therefore it pays to recruit new members by increasing group productivity, or even by 'kidnapping' members of other groups, as observed in white-winged choughs (*Corcorax melanorhamphos*). In this species adult 'kidnappers' herd fledglings from another territory into their own territory, where these young will later become unrelated helpers. Another direct benefit that may be gained by helping to raise offspring is the accumulation of breeding experience, which allows individuals to be more productive when they gain a breeding position themselves (as observed in the Seychelles warbler). Alternatively, individuals may help only to avoid being evicted by the dominants ('pay to stay' hypothesis), whereby they would lose the benefits associated with remaining in a group while waiting for future breeding opportunities (Emlen, 1982). Indeed prolonged residency within a group can also enhance the probability that an individual ascends to the dominant breeding position itself (e.g. Stacey and Koenig, 1990; Solomon and French, 1997), or allow subordinates to gain resources through 'budding off' of a portion of the territory (Woolfenden and Fitzpatrick, 1984).

Resource Competition and Social Interactions

Although the assumption is that higher numbers of subordinates, that are either helpers or co-breeders, have a positive effect on the reproduction or survival of the group, there may also be disadvantages of living in larger groups. The decision to remain or disperse is not, however, a unilateral one. Subordinate group members may compete with dominant group members for mates or food. Large groups may attract more predators, have a higher risk of parasite or disease infection and increased competition for food, which may lead to reduced survival and reproduction of group members. For example, in the Seychelles warbler adult birds living in larger groups had lower survival. With an increasing number of subordinates, the fitness benefit of helping (per subordinate) may also decline, and the option of dispersing may then prove more successful. However, dominant group members may force subordinates to disperse when the costs of having subordinates in the group exceed the benefits. Whether or not eviction occurs, and who is targeted is, at least in part, dependent on relatedness between group members. Dominant individuals may be more tolerant towards independent young to which they are directly related, as the natal territory functions as a safe haven where young have a higher chance of surviving. Moreover, the ability of young to successfully acquire a breeder vacancy may be facilitated by being allowed to wait on the safe natal territory until one becomes available. In such systems the kin benefits of allowing young to remain are reduced, or absent, for dominant individuals less related to the young, whereas the costs of group living remain. Consequently, dominants that are unrelated to the group young are more likely to evict young. This is most obvious when territories get taken over by new dominants, as for example in African lions (*Panthera leo*) and white-faced capuchins (*Cebus capucinus*), where takeovers result in the immediate killing or eviction of unrelated young. This is not to say that related dominant individuals are always tolerant. For example, in the superb fairy-wren any female offspring still in the natal territory at the start of the next breeding season are forced by the mother to disperse. Overall it is clear that in cooperative breeding systems those individuals that remain as subordinates may only be able to do so because the dominant group members allow them to.

That members of cooperatively breeding groups are often related may also affect dispersal in another way. When a dominant individual dies or disappears, group young of the same sex may attempt to occupy the vacant breeding position. If the parent of the opposite sex is still alive and dominant this pattern of inheritance would result in incestuous mating, which may lead to decreased fitness. To avoid this young should be selective when it comes to territory inheritance. In the Florida scrub-jay (*Aphelocoma coerulescens*), territory inheritance occurs more often when the surviving breeder is a stepparent of the potential heir rather than its natural parent. Similarly, males of *Antechinus agilis*, a small size dimorphic carnivorous marsupial, are more

likely to remain philopatric if the mother is removed at the time of weaning. In the acorn woodpecker, the red-cockaded woodpecker and the superb fairy-wren, dominants have even been observed to give up their breeder positions when all the opposite sex members of the group are closely related to them (Koenig and Dickinson, 2004). These results show that incest avoidance can lead to individuals giving up breeding opportunities and, therefore, to increased dispersal in an attempt to find other breeding vacancies with unrelated individuals. At a less facultative level, the evolution of general sex-biased patterns of dispersal may also have evolved to avoid inbreeding. Indeed although sex-biased dispersal is almost ubiquitous in vertebrates it appears to be especially pronounced in cooperative breeders.

An alternative way that females can avoid incestuous mating with related group members is through extra-group paternity, which, as stated above, can be relatively common. However, this means that in cooperative groups there can be a conflict of interest between dominant females that wish to gain extra-group paternity, and the dominant males and helping subordinates of either sex that may gain by protecting within-group paternity. How these conflicting interests are resolved within groups remains undetermined. Furthermore, if and how extra-group paternity has evolved to prevent inbreeding is also not clear, as several species in which extra-pair paternity frequently occurs still have high levels of inbreeding (Seychelles warbler), or avoid inbreeding by other behavioural mechanisms (superb fairy-wren).

Social Behaviour and Population Dynamics

Survival, reproduction and dispersal are the key processes regulating numbers and, thereby, population dynamics. Increasing population density usually has negative feedback effects on these demographic rates. Behaviour can also be affected; as density increases breeding vacancies become rare and individuals have to delay reproduction, thus promoting cooperative breeding (Emlen, 1982). Cooperative breeding might, in turn, affect the way that density dependence shapes demographic rates; higher density may be advantageous if individuals survive or reproduce better in larger cooperative groups (e.g. Brown, 1987; Clutton-Brock, 2002). However, whether an association between group size and reproduction/survival is a direct result of helping is difficult to determine as the decision to become a subordinate might depend on the quality of the territory or parents. Furthermore, high-quality breeders are likely to have larger groups because of past success, resulting in a noncausal correlation between the presence of subordinates and productivity. However, experiments in which helpers were removed have indicated that the relationship between reproductive success and group sizes can be a consequence of helping (e.g. in the grey crowned babbler, (*Pomatostomus temporalis*), Florida scrub-jay, Seychelles warbler and the Lake Tanganyika cichlid).

Although helping subordinates can improve the fitness of the other group members, in most species they are not essential for reproduction or survival. However, in obligate cooperative breeders, such as the white-winged chough, wild dog, (*Lycan pictus*), banded mongoose, (*Mungos mungo*), and dwarf mongoose, (*Helogale parvula*), the need for subordinates has become a constraint. If group size in these species falls below a critical number the population growth rate decreases, thus showing inverse density dependence.

At a larger scale cooperative breeding may act as a buffer against population fluctuations in periods of high mortality. Subordinates quickly occupy breeding vacancies when these become available, preventing any reduction in the size of the breeding population. Consequently, group living may buffer the negative effects of environmental or demographic stochasticity and make populations more resilient to such effects, an idea that has been supported by theoretical models on both the red-cockaded woodpecker and the African wild dog. In group living species competition over the limited number of territories and mates also restricts mate choice and can result in individuals pairing up with close family. The detrimental effects of such inbreeding may have deleterious effects on the persistence of groups and populations.

Interactions with Other Species

Living and cooperating in groups will affect how a species interacts with other species. Cooperating animals may benefit in that they have an advantage of numbers in intra-specific resource competition, they may also be better able to defend themselves or their young from species that prey on them, or may themselves be better at preying on other species. It has even been suggested that sociality has driven cognitive evolution in some species, thus providing general problem-solving abilities that enhance the ability of these animals to sequester and utilize resources, enabling them to outcompete or dominate other species (reviewed in Byrne and Bates, 2007). However (as discussed earlier), cooperative breeding may affect interactions in a manner that has negative impacts on the survival of individuals and thus the persistence of social species.

Clearly sociality and cooperation may affect interactions with other species, but it is also important to realize that these behaviours may be the consequence of such interactions. For example, individuals may initially form groups to avoid predation, either because of safety in numbers or because they group around an 'umbrella' species that helps protect them from predators. For example, northern orioles (*Icterus galbula bullockii*) cluster their nests around larger yellow-billed magpies (*Pica nuttali*) as they afford protection against nest predation by other corvids. Close aggregations of conspecifics formed in these ways may then facilitate the evolution of social interactions and cooperation. Indeed 'crecheing behaviour', where fledglings from a number of nests are looked after in a single group, has

only been observed in areas where the inter-specific nest predation described above occurs. From the brief discussion above it is clear that understanding how sociality and cooperation effects intra-specific interactions is an extremely complicated concept, one that has, to our knowledge, been the focus of relatively little research.

Conclusions

That some individuals spend part, or all, of their lives helping others to reproduce contradicts the concept of 'selfish' natural selection and provides an intriguing evolutionary paradox. When and why such apparently altruistic behaviour occurs has been the focus of this review. Although constraints and the benefits of group living, may persuade individuals to remain as subordinates, not only indirect 'kin' benefits but also direct benefits (such as becoming a breeding helper) appear to drive the evolution and maintenance of cooperative breeding. Cooperative behaviour can have wide-ranging consequences, not only on the biology of the cooperative species, but also on those species it interacts with.

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