



REVIEW

Ecological constraints, life history traits and the evolution of cooperative breeding

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The ecological constraints hypothesis is widely accepted as an explanation for the evolution of delayed dispersal in cooperatively breeding birds. Intraspecific studies offer the strongest support. Observational studies have demonstrated a positive association between the severity of ecological constraints and the prevalence of cooperation, and experimental studies in which constraints on independent breeding were relaxed resulted in helpers moving to adopt the vacant breeding opportunities. However, this hypothesis has proved less successful in explaining why cooperative breeding has evolved in some species or lineages but not in others. Comparative studies have failed to identify ecological factors that differ consistently between cooperative and noncooperative species. The life history hypothesis, which emphasizes the role of life history traits in the evolution of cooperative breeding, offers a solution to this difficulty. A recent analysis showed that low adult mortality and low dispersal predisposed certain lineages to show cooperative behaviour, given the right ecological conditions. This represents an important advance, not least by offering an explanation for the patchy phylogenetic distribution of cooperative breeding. We discuss the complementary nature of these two hypotheses and suggest that rather than regarding life history traits as predisposing and ecological factors as facilitating cooperation, they are more likely to act in concert. While acknowledging that different cooperative systems may be a consequence of different selective pressures, we suggest that to identify the key differences between cooperative and non-cooperative species, a broad constraints hypothesis that incorporates ecological and life history traits in a single measure of 'turnover of breeding opportunities' may provide the most promising avenue for future comparative studies.

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Cooperative breeding is a reproductive system in which more than a pair of individuals show parent-like behaviour towards young of a single nest or brood. Numerous variations have been identified including helping-at-the-nest by nonbreeding offspring that have delayed dispersal and remained with their parents on their natal territory, and various forms of cooperative polygamy or plural breeding in which more than a single male or female share breeding status within the same social unit. Aid generally consists of feeding nestlings or fledglings, but can also include incubation and defence of

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the nest or territory, and the aid-givers or cobreeders are often related to the focal breeding pair (Brown 1987). The evolution of cooperative breeding can usually be broken down into two complementary processes: the decision to stay in the natal unit and the decision to help. Thus, research has traditionally focused on two questions: 'Why delay dispersal?' and 'Why help?' Helping is not an inevitable consequence of delayed dispersal (e.g. Gayou 1986; Veltman 1989; Ekman et al. 1994) but in the majority of cooperatively breeding species, delayed dispersal is a prerequisite for helping behaviour.

The fitness benefits of helping are well documented. Helpers can increase their inclusive fitness by gaining either indirect fitness benefits from helping close relatives to increase the number of their genes in future generations, or direct fitness benefits from increased

future personal reproduction (for reviews see Emlen 1991; Cockburn 1998). However, in most species the fitness benefit from helping is likely to be considerably less than the potential direct genetic gain from immediate independent breeding if a territory and mate could be obtained (Brown 1987). Thus cooperative behaviour can be seen as a 'best-of-a-bad-job' strategy, adopted when opportunities for independent breeding are limited. Therefore, understanding why grown offspring delay dispersal is the key to understanding the evolution of cooperative breeding.

The first explanation for the delayed dispersal of grown offspring was developed by Selander (1964) in a study of *Campylorhynchus* wrens. Selander (1964) proposed that a lack of breeding territories prevented the dispersal of grown offspring: the habitat saturation hypothesis. This idea was elaborated by various workers (Brown 1974; Gaston 1978; Stacey 1979; Koenig & Pitelka 1981), and has since been expanded to encompass a range of ecological and demographic constraints on dispersal besides a shortage of suitable territories: the ecological constraints hypothesis (Emlen 1982, 1984). Constraints on independent breeding have been found to act in four ways: (1) a shortage of vacant breeding territories of sufficient quality for independent breeding; (2) a high mortality risk associated with dispersal; (3) a low probability of finding a mate; and (4) a low chance of successful independent reproduction once a territory has been established.

The ecological constraints hypothesis is now widely accepted as the explanation for the evolution of delayed dispersal (Koenig et al. 1992; Emlen 1994, 1997; but see Cockburn 1996), although alternative hypotheses have been put forward. The benefits of philopatry hypothesis (Stacey & Ligon 1987, 1991; Waser 1988) proposed that delayed dispersal was not a consequence of extrinsic constraints, but of intrinsic benefits gained by remaining on the natal territory. In other words, if variation in habitat quality increases the benefits of philopatry, cooperative breeding can be found even in the absence of habitat saturation. The distinction between these two models has been much debated in the literature (Heinsohn et al. 1990; Zack 1990; Emlen 1991; Koenig et al. 1992; Walters et al. 1992), but the benefits of philopatry hypothesis has now been accommodated successfully within the ecological constraints hypothesis by the recognition that they differ only in the emphasis they place on either the costs of leaving or the benefits of staying (Koenig et al. 1992; Mumme 1992; Emlen 1994, 1997; but see Ligon 1999). Both hypotheses are based on the assumption that a cost-benefit analysis of leaving versus staying is resolved in favour of the latter option. Cockburn (1996) has pointed out that it is important to consider this cost-benefit analysis from the point of view of adults as well as their young. Parental aggression rather than the wishes of offspring may determine whether or when dispersal occurs.

It has long been postulated that certain life history characteristics, such as high juvenile and adult survival, may also play a role in the evolution of cooperative breeding by creating a surplus of individuals in a given habitat (Brown 1974, 1987; Ricklefs 1974; Fry 1977;

Russell 1989; Rowley & Russell 1990). The life history hypothesis explains the expression of cooperative behaviour in some taxonomic lineages but not others on the basis of life history traits. This hypothesis has gained recent prominence through a comparative analysis by Arnold & Owens (1998) in which low adult mortality and low dispersal were found to be the key factors predisposing certain avian lineages to show cooperative breeding.

Our aim in this paper is to review and evaluate the different kinds of evidence for the ecological constraints hypothesis, and to discuss whether the life history hypothesis provides an alternative explanation for why cooperative breeding has evolved in some lineages but not in others. In other words, we address the question of whether there are consistent differences between cooperative and noncooperative species in terms of either their ecology or their life history traits. Our review focuses on birds, primarily because avian studies have played a pre-eminent role in this field. The ideas discussed, however, are also applicable to other cooperatively breeding vertebrates and invertebrates.

THE ECOLOGICAL CONSTRAINTS HYPOTHESIS

Intraspecific Studies

The strongest support for the ecological constraints hypothesis as an explanation for the evolution of delayed dispersal is provided by intraspecific studies. A positive association between the severity of constraints and the prevalence of cooperative behaviour has been observed in comparisons across populations or across years in the same species (Emlen 1984). Numerous studies have identified the critical constraints: a shortage of territory vacancies (e.g. Emlen 1984; Woolfenden & Fitzpatrick 1984), high dispersal costs (Ligon & Ligon 1990; DuPlessis 1992; Russell 1999), a shortage of breeding partners (e.g. Rowley 1965, 1981; Maynard Smith & Ridpath 1972; Reyer 1984; Clarke 1989; Marzluff & Balda 1990; Walters et al. 1992), and a low probability of successful breeding once a territory has been obtained (e.g. Reyer 1980; Emlen 1982; Stacey & Ligon 1987; Curry 1988).

These observational studies are consistent with the ecological constraints hypothesis, but they do not demonstrate causation. More rigorous support comes from experimental studies in which constraints are artificially relaxed. Experimental removal of breeders results in helpers of the same sex as the removed birds abandoning helping and moving to occupy the vacant breeding opportunities. Families of superb fairy wrens, *Malurus cyaneus*, consist predominantly of parents and grown sons. The creation of male breeding vacancies through removal of breeding males caused the dissolution of family groups, with mature nonbreeding sons leaving home to fill these vacancies. However, when vacant territories without a breeding partner were created by removal of the breeding pair, male helpers did not disperse until the missing female breeder was returned to her territory (Pruett-Jones & Lewis 1990). Therefore, habitat and mate availability are both important constraints in

this species. Analogous results have been reported for red-cockaded woodpeckers, *Picoides borealis* (Walters 1991; Walters et al. 1992), where the provision of new nest sites induced helpers to leave home and establish breeding territories. Similarly, the creation of breeding vacancies in the Seychelles warbler, *Acrocephalus sechellensis* (Komdeur 1992), resulted in helping offspring leaving home to assume breeder status. However, in this case, offspring only filled vacancies on territories that were of equal or higher quality than their natal territories. This makes sense because the fitness benefits of breeding independently exceed those of helping on their natal territories only when the breeding territory is of equal or better quality than the helping territory (Komdeur 1992).

Thus, observational and experimental studies of single species have strongly supported the ecological constraints hypothesis. However, to provide a comprehensive explanation for the evolution of cooperative breeding any hypothesis must explain why cooperative breeding has evolved in some species or lineages, but not in others (Smith 1990; Koenig et al. 1992). Here, the ecological constraints hypothesis has proved less successful. The difficulty arises because it is clear that ecological constraints are ubiquitous in nature, so individuals of most species encounter constraints on their preferred breeding options (Heinsohn et al. 1990; Stacey & Ligon 1991; Newton 1992, 1998). Despite this, cooperative breeding is known in only 3.2% of extant bird species (308 cooperative species out of a total of 9672 species; Sibley & Monroe 1990; Arnold & Owens 1998). In noncooperative species, constraints may be reflected by the existence of individuals who adopt floating or queuing strategies, rather than becoming helpers (Smith 1978; Koenig et al. 1992; Zack & Stutchbury 1992; Kokko & Sutherland 1998). For example, in the oystercatcher, *Haematopus ostralegus*, a shortage of good breeding territories causes many offspring to disperse, delay reproduction and queue for good-quality vacancies. The delay in reproduction is balanced by higher reproductive success once they do breed (Ens et al. 1992, 1995). Although such species share features with most cooperatively breeding species (long lived, saturated habitat, surplus adults), cooperative breeding is absent. However, even within systems in which nonbreeding adults delay dispersal and remain on their natal territory in families, subsequent helping behaviour is not universal (e.g. green jays, *Cyanocorax yncas*: Gayou 1986; Australian magpies, *Gymnorhina tibicen*: Veltman 1989; Siberian jay, *Perisoreus infaustus*: Ekman et al. 1994). Indeed, even within routinely cooperative species some individuals may adopt a floating rather than a helping strategy (e.g. red-cockaded woodpecker: Walters et al. 1992; Seychelles warbler: Komdeur 1991; pukeko, *Porphyrio porphyrio*: Craig & Jamieson 1990; hoatzin, *Opisthocomos hoazin*: Strahl & Schmitz 1990).

Interspecific Studies

It is obvious from the previous section that there is a continuum of dispersal strategies among birds. This is explicit within the framework of the delayed dispersal

threshold model (Koenig et al. 1992) which contrasts the fitness consequences of dispersal and independent breeding, dispersal and floating and delayed dispersal and helping strategies. Koenig et al. (1992) emphasized that given the ubiquity of constraints on preferred breeding options, it is just as important to ask why a species is not cooperative, as it is to ask why a species is cooperative. The problem lies in the fact that ecological constraints of one kind or another can very often be identified and invoked as being the causal factor in studies of a given cooperatively breeding species. The goal of interspecific studies is to identify common factors that promote the evolution of cooperation in some species, but not in others.

Comparisons of closely related species have highlighted differences between cooperative and noncooperative species that are consistent with the ecological constraints hypothesis. Bell & Ford (1986) compared the ecology of three species of Australian thornbill, *Acanthiza*, two of which are cooperative. They suggested that the dense foraging habitat of the noncooperative species reduced the benefits of group vigilance and thus tipped the balance in favour of noncooperation. Similarly, Noske (1991) suggested that in the three species of Australian treecreepers (Climacteridae), the cooperative behaviour of two species was attributable to specialized niche requirements and limiting resources, which together acted as a constraint on dispersal. Finally, a comparison of two sympatric species of *Lanius* shrikes by Zack & Ligon (1985) found that the cooperative common fiscal shrike, *L. collaris*, had more stable territories and lower breeder turnover than the noncooperative grey-backed fiscal shrike, *L. excubitorius*. These differences were attributed to the occupation of stable, high-quality, but restricted habitat by the common fiscal shrike.

Such comparisons suggest a link between cooperative breeding, habitat saturation and habitat characteristics, but they suffer from the weakness that the identification of constraints is often post hoc and the explanation for the evolution of cooperative behaviour still tends to be at a species-specific level. The challenge is to identify covariates of cooperative breeding that can explain the evolution of this behaviour on a broad geographical and taxonomic scale.

It has long been apparent that there is marked geographical variation in the occurrence of cooperative breeding. Polar and north temperate regions have few cooperative species, while cooperative breeding is relatively common in the tropics, and is most prevalent in Australia, where at least 10% of all bird species breed cooperatively (Rowley 1976; Dow 1980; Brown 1987; Russell 1989). This distribution suggests the existence of either environmental or phylogenetic effects on the evolution of cooperative breeding. We consider the role of phylogeny in the next section, but first we ask how successful comparative studies have been at identifying ecological correlates of cooperative breeding.

Australian birds have naturally been the subject of several comparative analyses. Dow (1980) detected no clear relationship between environmental factors and cooperative breeding, but Ford et al.'s (1988) analysis

suggested that a limit on cooperative breeding was set by a minimum level of food abundance through the year. They found that cooperative breeding was most common among insectivorous species inhabiting areas with stable, aseasonal insect populations, while noncooperative insectivores lived in seasonal habitats. Ford et al.'s (1988) finding that a lack of seasonality promoted cooperation supported the contention of Rowley (1968) that cooperative breeding was possible only where food was plentiful throughout the year. However, Cockburn (1991) re-analysed Ford et al.'s (1988) data, while controlling for phylogeny (Harvey & Pagel 1991), and found no relationship between foraging mode and the occurrence of cooperation. Instead, Cockburn (1996) suggested that the main ecological pattern in the occurrence of cooperation within the Corvida, a large group of passerines that originated in Australia (Sibley & Ahlquist 1990), is the tendency for noncooperative species to be found in dense, visually occluded habitats. It was argued that group cohesion is difficult to maintain in such habitats. Cockburn (1996) concluded that the cooperative behaviour of many Australian species 'cannot be reconciled with the habitat saturation model, or the peculiar habitat or social constraints faced by the species which were used to derive that model'.

In contrast to Ford et al.'s (1988) study of Australian cooperative species, a comparative analysis of South African birds by DuPlessis et al. (1995) found that cooperative breeding was associated with seasonal environments. This analysis distinguished between regular and occasional cooperative breeders, and it was suggested that regular cooperative breeders live in open savannah habitats where predation pressure favours group living and where food supplies during the non-breeding season never fall below a baseline level. Occasional cooperative breeders were found to live in highly unpredictable environments where cooperation occurs only when conditions are too bad for independent reproduction. One factor that might influence the probability of successful independent breeding is the probability of nest predation, but Poiani & Pagel (1997) found no evidence to support the idea that cooperative breeding was related to nest predation among Australian birds.

A recent comparative analysis by Arnold & Owens (1999) is the most comprehensive in terms of species number and the most sophisticated in terms of analytical techniques. At the level of species or genus, cooperative breeding was found to be associated with reduced adult dispersal and group living during the breeding season. Disentangling cause and effect in these traits is obviously difficult, but Arnold & Owens (1999) also found that cooperative breeding was associated with warm winters and low temperature variation. Feeding ecology was not related to cooperation. Interestingly, analyses at the family level revealed little evidence for a link between ecology and cooperative breeding. Arnold & Owens (1999) concluded that while ecological differences may explain the occurrence of cooperation among closely related species, ecology acts as a facilitator only within certain lineages that are predisposed to be cooperative,

the predisposition occurring through the evolution of certain life history traits (see next section).

If any general conclusion can be drawn from these comparative studies, it must be that although there are some common themes (e.g. aseasonality) they have failed to identify ecological factors that differ consistently between cooperative and noncooperative breeders. In this respect, the ecological constraints hypothesis, as tested in these comparative studies, does not provide a comprehensive model for the evolution of delayed dispersal and helping because there is little predictive power in the current formulation of the hypothesis (Cockburn 1996, 1998). The difficulty in identifying ecological correlates of cooperation and in demonstrating that cooperative breeders are more constrained than noncooperative breeders has led to a closer examination of other potential correlates, in particular phylogeny and life history traits.

THE LIFE HISTORY HYPOTHESIS

In contrast to the ecological constraints hypothesis, the life history hypothesis emphasizes the role of life history traits, such as clutch size, dispersal and longevity, in the evolution of cooperative breeding. It has been proposed that the life history strategies of cooperative breeders are biased towards the *K*-selected end of the *r*-*K* continuum, being characterized by delayed maturity, high adult survival, and low reproductive and dispersal rates (Brown 1974, 1987; Fry 1977; Gaston 1978; Russell 1989; Rowley & Russell 1990; Poiani & Jermiin 1994; Arnold & Owens 1998). Indeed, Ricklefs (1974) suggested that cooperative breeding evolved in a particular demographic context where recruitment exceeded the death rate, the resulting competition favouring the evolution of delayed reproduction. Ecological theory predicts that these *K*-selected traits will exist in predictable environments supporting stable populations (MacArthur & Wilson 1967; Pianka 1970), echoing Ford et al.'s (1988) finding that cooperative breeders occurred in aseasonal environments.

Life history traits have been highly conserved in avian evolution (Owens & Bennett 1995), so the well-documented phylogenetic bias in cooperatively breeding species (Russell 1989; Edwards & Naem 1993; Cockburn 1996) is consistent with the life history hypothesis. Phylogenetic analyses are greatly facilitated by the existence of a consistent and comprehensive avian phylogeny (Sibley & Ahlquist 1990), and the clumped taxonomic distribution of cooperative breeders is apparently robust despite the partial information that is available on the breeding system of many avian taxa (Cockburn 1996).

Early attempts to identify life history correlates of cooperation were equivocal in their support of the hypothesis. Selective comparisons by Rowley & Russell (1990) suggested that longevity may act as an important extrinsic constraint on the occurrence of breeding opportunities. However, in a more extensive analysis Yom-Tov et al. (1992) failed to find a relationship between cooperative breeding and longevity in Australian birds. Similarly, in the first systematic analysis of life history traits in cooperative and noncooperative species, Poiani

& Jermiin (1994) failed to find any consistent differences in clutch size and longevity in the Australian Corvida.

In contrast to these studies, a recent comparative analysis on a global scale (79 cooperative and 103 non-cooperative species, representing 139 families) by Arnold & Owens (1998) identified several important patterns: (1) cooperative breeding is restricted to certain families; (2) the level of cooperative breeding is strongly associated with low adult mortality and small clutch size; (3) this low adult mortality rate is associated with increased sedentariness, lower latitudes and reduced environmental fluctuation; and (4) the proportion of cooperatively breeding species per family is correlated with a low family-typical value of annual mortality. This last result was interpreted as showing that low mortality predisposes a lineage to cooperative breeding rather than vice versa. This is important because without this key result it is quite reasonable to argue that reduced mortality is a consequence of cooperative breeding via the benefits of delayed dispersal and group living. Therefore, Arnold & Owens (1998) concluded that the key factor that predisposes certain avian lineages to cooperative breeding is low annual mortality. They suggest that population turnover may be slowed further by ecological changes such as becoming sedentary and a reduction in the opportunities for independent breeding. Living in a relatively stable climate allows year-round territory occupation, and the low population turnover and reduced dispersal result in a 'saturated' environment. This is consistent with most cooperative species being found in tropical and subtropical regions. Therefore, the life history hypothesis offers a combination of a life history predisposition to delayed dispersal and cooperative breeding, and ecological facilitation (Arnold & Owens 1998). In other words, within predisposed taxonomic lineages, cooperative breeding will occur given the appropriate ecological conditions. Habitat becomes saturated because of a low turnover in population rather than any particular feature of the species' ecology. This model has considerable utility as a depiction of the evolutionary route to cooperation and as an explanation for the patchy phylogenetic distribution of cooperative breeders.

LIFE HISTORY VERSUS ECOLOGICAL CONSTRAINTS

We now ask whether the life history and ecological constraints hypotheses are really distinct, acting at different taxonomic levels, or whether they act in conjunction to determine whether a species breeds cooperatively. The key difference between the two is that the life history hypothesis proposes that in general cooperative breeding will be expressed only in those lineages with the appropriate life history traits. In contrast, the ecological constraints hypothesis suggests that any species might be persuaded to breed cooperatively if put in the appropriate environment. The fundamental question in this context concerns the plasticity or facultative nature of cooperative breeding. The debate over the origin and maintenance of cooperative breeding has been well rehearsed in the literature (e.g. Jamieson 1989, 1991; Emlen et al.

1991), and it is clear from phylogenetic analyses that cooperative breeding is not necessarily a conserved trait. For example, a study on the phylogeny of social evolution in the *Aphelocoma* jays showed that cooperative breeding predated radiation of the genus but was subsequently lost in at least two lineages (Peterson & Burt 1992). Similarly, a study of four closely related *Acrocephalus* warblers (Leisler et al. 1997) found one to be a noncooperative breeder, two facultatively cooperative breeders, and one to be facultatively polygynous (Komdeur 1999). Finally, the ecologically and taxonomically similar Galapagos hawk, *Buteo galapagoensis*, and Harris hawk, *Parabuteo unicinctus*, have social groups that are widely divergent in composition, stability and function, the former being cooperatively polyandrous, and the latter having helpers at the nest (Faaborg & Bednarz 1990).

Very few species can be described as obligate cooperative breeders (e.g. white-winged chough, *Corcorax melanorhamphos*: Heinsohn 1992), and in virtually every study of cooperative species a proportion of the population breeds in the typical avian system of monogamy (Emlen 1991). Furthermore, there may be considerable variation in social organization within the proportion of a population that is cooperative. This variation encompasses related and unrelated helpers-at-the-nest, monogamy, polygyny, polyandry and polygynandry (e.g. acorn woodpeckers, *Melanerpes formicivorus*: Koenig & Mumme 1987; pied kingfishers, *Ceryle rudis*: Reyer 1990; Seychelles warbler: Komdeur 1991; dunnocks, *Prunella modularis*: Davies 1992). Thus, the social system of cooperative species is clearly not fixed, and the same is certainly true of many noncooperative species (e.g. Møller 1986). According to the life history hypothesis any noncooperative species within a cooperative lineage might be expected to show cooperative behaviour given the right ecological circumstances. The important question is whether this is also true of noncooperative species within noncooperative lineages. To our knowledge, no study has attempted to induce cooperative behaviour in noncooperative species from noncooperative lineages by manipulation of constraints. Nevertheless there are many examples in the literature of occasional helping behaviour in ostensibly noncooperative species (e.g. Arctic tern, *Sterna paradisea*: Skutch 1961; barn swallow, *Hirundo rustica*: Myers & Waller 1977; European blackbirds, *Turdus merula*: Dijkstra et al. 1997; European starling, *Sturnus vulgaris*: J. Komdeur & P. Wiersma, personal observation; European robin, *Erithacus rubecula*: Harper 1985; Galapagos finches, *Geospiza* spp.: Price et al. 1983; white-fronted geese, *Anser albifrons*: Fox et al. 1995; European kestrel, *Falco tinnunculus*: E. Dijkstra, personal communication), several of which come from supposedly noncooperative lineages (Arnold & Owens 1998). There was no evidence in any of these examples that helping resulted from polyandrous mating, but nor was it known whether the helping behaviour was a consequence of unusual or atypical constraints on reproductive options.

In the light of the facultative nature of cooperative breeding, the acquisition and loss of cooperative behaviour within lineages, and the evidence of occasional cooperation within apparently noncooperative species,

we believe that the distinctions between cooperative and noncooperative lineages are less clear than is suggested by the life history hypothesis. In addition, as recognized by Arnold & Owens (1998), there are exceptions to both hypotheses for the expression of cooperative behaviour. For example, the cooperatively breeding long-tailed tit, *Aegithalos caudatus*, has low adult survival (57%) and no habitat saturation (Hatchwell 1999; Hatchwell et al. 1999). Similarly, the survival rates of the cooperatively breeding European bee-eater, *Merops apiaster* (mean annual adult survival 34%; Lessells 1990), western bluebird, *Sialia mexicana* (50%; Dickinson et al. 1996), and pygmy nuthatch, *Sitta pygmaea* (57%; Sydean et al. 1988), are relatively low. On the other hand, many species with very high survival rates and delayed reproduction, traits common in cooperative breeders, do not show cooperative breeding, e.g. oystercatcher (88%; Heg & van Treuren 1998); Seychelles fody, *Foudia sechellarum* (81%; Brooke 1985; K. Kraaijeveld & J. Komdeur, unpublished data) and most seabirds (Nelson 1980; Ollason & Dunnett 1988). Furthermore, of over 250 species of hawks (order Falconiformes) and almost 140 species of owls (order Strigiformes), fewer than a dozen species possess some form of group breeding (Faaborg & Bednarz 1990). It is unrealistic to expect that every exceptional instance of cooperation or noncooperation will be accommodated within a single model, but such cases do serve to illustrate the fact that in addition to the pronounced variation across populations, species or lineages, there is also considerable variation within these levels.

Therefore, rather than regarding life history traits as predisposing, and ecological factors as facilitating cooperation, we suggest that they are more likely to act in concert by influencing the rate of turnover of suitable breeding opportunities. Turnover and the occupation of vacant breeding territories by helpers will depend on breeder survival rate (a life history trait) and the degree of habitat saturation (an ecological constraint). The latter will often be reflected in the number of competitors for a breeding vacancy. Therefore, we suggest that the distinction between the life history and ecological constraints hypotheses is artificial, and that in contemporary empirical studies that seek functional explanations of cooperative behaviour a broad constraints hypothesis that incorporates ecological and life history traits stands a more realistic chance of identifying the selective pressures resulting in cooperative breeding than either hypothesis in isolation. Future comparative studies that seek ecological and/or demographic correlates of cooperative breeding should attempt to formalize a broad constraints hypothesis that combines both ecological and life history parameters into a single measure of turnover of breeding opportunities. To some extent this has long been recognized because although Emlen (1982) did not mention life history traits specifically in his original formulation of the ecological constraints hypothesis, he did stress that competition for breeding vacancies was 'dependent upon the population density, and the number and turnover rate of territory vacancies', thereby implying the importance of demographic constraints.

Finally, it is important to note that we do not assume that analyses that combine both life history and ecological traits will necessarily provide a comprehensive explanation for the evolution of delayed dispersal in all cooperative species because it seems likely that different cooperative systems may be a consequence of different selective pressures (e.g. Hartley & Davies 1994; Cockburn 1996, 1998) and there are always likely to be exceptional cases requiring species- or taxon-specific explanations. Nevertheless, we suggest that an analysis of this sort stands the best chance of identifying the key differences between cooperative and noncooperative species.

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