Cooperative breeding in birds: a comparative test of the life history hypothesis

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In approximately 3.2% of bird species individuals regularly forgo the opportunity to breed independently and instead breed cooperatively with other conspecifics, either as non-reproductive 'helpers' or as co-breeders. The traditional explanation for cooperative breeding is that the opportunities for breeding independently are limited owing to peculiar features of the species' breeding ecology. However, it has proved remarkably difficult to find any common ecological correlates of cooperative breeding in birds. This difficulty has led to the 'life history hypothesis', which suggests that the common feature of cooperatively breeding birds is their great longevity, rather than any particular feature of their breeding ecology. Here, we use a comparative method to test the life history hypothesis by looking for correlations between life history variation and variation in the frequency of cooperative breeding. First, we find that cooperative breeding in birds is not randomly distributed, but concentrated in certain families, thus supporting the idea that there may be a common basis to cooperative breeding in birds. Second, increases in the level of cooperative breeding are strongly associated with decreases in annual adult mortality and modal clutch size. Third, the proportion of cooperatively breeding species per family is correlated with a low family-typical value of annual mortality, suggesting that low mortality predisposes cooperative breeding rather than vice versa. Finally, the low rate of mortality typically found in cooperatively breeding species is associated with increasing sedentariness, lower latitudes, and decreased environmental fluctuation. We suggest that low annual mortality is the key factor that predisposes avian lineages to cooperative breeding, then ecological changes, such as becoming sedentary, further slow population turnover and reduce opportunities for independent breeding. As the traditional explanation suggests, the breeding habitat of cooperatively breeding species is saturated, but this saturation is not owing to any peculiar feature of the breeding ecology of cooperative breeders. Rather, the saturation arises because the local population turnover in these species is unusually slow, as predicted by the life history hypothesis.

Keywords: cooperative breeding; habitat saturation; mortality; life history; comparative methods; birds

1. INTRODUCTION

Why, in some species of bird, such as the dunnock (*Prunella modularis*) and the green woodhoopoe (*Phoeniculus purpureus*), do individuals regularly forgo the opportunity to breed independently and instead breed cooperatively with other conspecifics? The widely accepted answer to this question, often called the 'habitat saturation' hypothesis, is that those individuals who forgo, or share, their reproductive attempt cannot breed elsewhere because of a shortage of breeding opportunities (see, for example, Selander 1964; Brown 1974, 1987; Gaston 1978; Stacey 1979; Koenig & Pitelka 1981; Emlen 1982, 1984, 1991; Emlen & Vehrencamp 1985; Koenig *et al.* 1992) and cannot become floaters owing to a lack of marginal habitat. Indeed, such habitat saturation has been demonstrated convincingly using experimental manipulations (see, for example, Pruett-Jones & Lewis 1990; Komdeur 1992).

The habitat saturation hypothesis, while conceptually useful, is really just a proximate explanation of cooperative breeding. The obvious question is, why are breeding opportunities more limited for cooperative than non-

cooperative species? Answers to this question are more controversial. The traditional explanation is that the suitable breeding habitat of cooperatively breeding species is saturated because they have peculiar features to their breeding ecology (Stacey 1979; Koenig & Pitelka 1981; Emlen 1982, 1984; Emlen & Vehrencamp 1985; Koenig & Mumme 1987; Koenig *et al.* 1992; Davies *et al.* 1995). For example, in the green woodhoopoe, nesting and roosting holes are thought to limit dispersal and breeding (Ligon & Ligon 1990). This explanation of habitat saturation via peculiarities of breeding ecology has strong intuitive appeal. However, while certain cooperatively breeding species, such as the green woodhoopoe, have obvious peculiar features of their breeding ecology which may predispose them to cooperative breeding, the case is not nearly so clear in other species (Smith 1990). Indeed, it has proven notoriously difficult to identify any common ecological correlates of cooperative breeding in birds (see, for example, Dow 1980; Ford *et al.* 1988; Du Plessis *et al.* 1995; Poiani & Pagel 1997), or to demonstrate that cooperatively breeding species are more 'ecologically constrained' than non-cooperative species (Smith 1990).

Due to this difficulty, some studies of cooperative breeding have shifted the emphasis from examination of

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variation in ecological factors *per se* to variation in life history traits (see, for example, Rowley 1974; Russell 1989; Rowley & Russell 1990, 1997). Specifically, it has been suggested that cooperative breeding tends to occur in species with low annual mortality because this leads to 'overcrowded' populations with little opportunity for the establishment of new breeding territories (Brown 1969, 1974, 1987; Russell 1989; Rowley & Russell 1990). This 'life history hypothesis' is, therefore, a subtle twist on the traditional explanation of habitat saturation in cooperatively breeding species. Whereas the traditional explanation suggests that breeding opportunities are limited by an absolute shortage of a peculiar form of, for example, nest site, the life history hypothesis suggests that breeding habitat saturation occurs because the turnover of territory owners is unusually slow.

The life history hypothesis, as summarized by Russell (1989; see also Brown 1969, 1974, 1987; Rowley & Russell 1997), has caused some comment (see, for example, Heinsohn *et al.* 1990; Koenig *et al.* 1992; Cockburn 1996), but relatively little precise quantitative analysis of the differences between cooperative and non-cooperative species (but see Brown 1974, 1987; Zack & Ligon 1985; Yom-Tov 1987). In a comprehensive review of cooperative breeding among Australian passerines, Cockburn (1996) concluded that 'there is no definite link between life history and cooperative breeding' (p. 466). Similarly, the only two explicit comparative studies of the life history hypothesis were unable to find a consistent difference in life history between cooperative and non-cooperative species of Australian passerine (Poiani & Jermiin 1994; Poiani & Pagel 1997).

Our study uses a modern comparative method to test the life history hypothesis. We aim to address four explicit questions. Is cooperative breeding randomly distributed among avian families? Are there consistent differences between cooperative and non-cooperative species in terms of their life history? Do cooperative species tend to occur in families that are predisposed to extreme life histories? What are the climatic and behavioural correlates of extreme life histories?

Our analyses concentrate on the life history hypothesis, rather than testing the plethora of hypotheses that have been put forward to explain cooperative breeding. Furthermore, we have grouped together different forms of cooperative breeding, such as cooperative monogamy and cooperative polygamy (see Hartley & Davies 1994), and do not even tackle the big question of why helping behaviour *per se* occurs. Despite these qualifiers, we believe our analysis is useful because it is, to our knowledge, the first test of the life history hypothesis based on quantitative, cross-species comparisons between large numbers of cooperative and non-cooperative species.

2. METHODS

The first question we addressed was, is cooperative breeding randomly distributed among avian families? We followed the traditional definition of cooperative breeding as any situation in which 'more than two individuals rear the chicks at one nest' (Emlen & Vehrencamp 1985), irrespective of the precise genetic mating system. We used Brown's (1987) list of cooperatively breeding birds, supplemented by Dow (1980), Du Plessis *et al.* (1995) and

Cockburn (1996) to form a list of potentially cooperatively breeding bird species. It was known that at least some of these entries were based on small sample sizes, but all were included at this stage to maximize the number of lineages represented and thereby provide a conservative test of the null hypothesis that cooperative breeding is randomly distributed among avian taxa.

Based on this list of potentially cooperatively breeding species, we calculated that cooperative breeding has been reported in at least 3.2% of extant bird species (308 cooperatively breeding species out of a total of 9672 species; Sibley & Monroe 1990). Next, we calculated the proportion of cooperatively breeding species in each of 139 families recognized by Sibley & Monroe (1990). Then, under the null hypothesis that cooperative breeding is distributed randomly among families, we calculated the binomial probability, R, that a family of N species contains k cooperatively breeding species, using the function $R = p^k (1 - p)^{N-k}$, where p is the overall proportion of species that are cooperative breeders (in this case $p = 0.032$). However, in their raw state, these probabilities are not suitable for significance tests because many multiple tests have been done. Instead, we calculated the adjusted critical value by using the Dunn–Sidak method (Sokal & Rohlf 1995). The value 3.60×10^{-4} was equivalent to the 5% confidence level. Any binomial probability less than this value indicates that the family in question contains significantly more, or significantly fewer, cooperative species than predicted by chance (see, for example, Bennett & Owens 1997). Unfortunately, because our knowledge of the breeding ecology of many species, particularly tropical species, is very limited, some of our tests are likely to be very conservative (see Cockburn 1996).

Our second question concerned the power of life history in explaining the frequency of cooperative breeding among birds. Here we used a modern comparative method to explore correlations between changes in the frequency of cooperative breeding and changes in indices of life history. Data were collated from the literature on 79 species of definitely cooperatively breeding birds and 103 species of non-cooperatively breeding birds. Wherever possible, each cooperatively breeding species was matched with one closely related and one more distantly related non-cooperatively breeding species from the same family. The database was also balanced by inclusion of species from well-studied families in which cooperative breeding has not been recorded. In total, 139 families were represented in the database.

For each species, frequency of cooperative breeding was scored on a four-point scale, depending on the percentage of nests at which more than two individuals contributed to the rearing of a single brood; 0 = less than 5% of nests cooperative (i.e. non-cooperative) (103 species in our database), 1 = 6–35% (32 species), 2 = 36–75% (24 species), 3 = 76–100% (23 species). A rank scale, rather than raw values, was used to minimize the effects of temporal and geographical variation in levels of, and our knowledge of, cooperative breeding.

Our two indices of life history variation were annual rate of mortality among breeding adults (per cent mortality per year) and modal clutch size. We included a measure of fecundity as an index of life history because, unlike estimates of mortality, clutch size can be measured directly and, as such, is not influenced by potentially confounding factors such as dispersal and migration. Furthermore, in a stable population, high survivorship would be balanced by reduced fecundity (Owens & Bennett 1995). Clutch size, rather than annual fecundity, was used as a measure of reproductive rate because for many species there is very little information on the modal number of clutches per year.

When addressing our second question, we anticipated that closely related species were likely to be more similar to one another with respect to behaviour and life history than expected by chance (see Harvey & Pagel 1991). Species could not, therefore, be used as independent data points. Hence, we controlled for the degree of common ancestry (see, for example, Harvey & Pagel 1991) by using the Comparative Analysis by Independent Comparisons (CAIC) software program (Purvis & Rambaut 1995) to identify and calculate evolutionarily independent contrasts (Felsenstein 1985; Pagel 1992). Our four-point scale of cooperative breeding was used as the dependent variable and our indices of life history and breeding ecology as the independent variables. As our cooperative breeding scores were discrete character states, a BRUNCH analysis was performed. This uses parsimony to identify the minimum number of changes necessary to account for the observed variation in the dependent variable, and then calculates changes in the independent variables at those nodes only (Purvis & Rambaut 1995). Two-tailed Wilcoxon signed-rank tests based on the independent contrasts were used to test for associations between changes in the level of cooperative breeding and changes in each independent variable. The Wilcoxon signed-rank test tests the hypothesis that, at nodes where the dependent variable increases, the independent variable is equally likely to increase or decrease (Owens & Hartley 1998).

We used the full Sibley & Ahlquist (1990) tapestry phylogeny as our phylogenetic topology for this and all subsequent analyses. Branch lengths at family level and above were set from Sibley & Ahlquist's (1990) tapestry phylogeny. Branch lengths between genera in the same family were all set at the arbitrary length of two, and between species in the same genus at one.

Our third question was whether variation among families in the proportion of cooperatively breeding species was correlated with variation among families in life history. For all families represented in the database, a value of clutch size and annual mortality was chosen randomly from an independent database of non-cooperative species (P. M. Bennett and I. P. F. Owens, unpublished data) as a representative value for that family. Family-typical values are a valid representation of life history variation among birds, because less than 5% of life history variation occurs within families (Owens & Bennett 1995). In total, eight families that contained no definitely non-cooperatively breeding species were excluded from this analysis because it is likely that cooperative breeding is the ancient state in these families. A new CAIC analysis was conducted to discover whether changes in the proportion of definitely cooperatively breeding species in a family were correlated with changes in the family-representative values of clutch size and annual mortality. CAIC's CRUNCH algorithm (Purvis & Rambaut 1995) was used to generate the contrasts at all phylogenetic nodes. Again, we used two-tailed Wilcoxon signed-rank tests to look for an association between changes in the frequency of cooperative breeding and changes in clutch size and breeder mortality rate.

Our final question referred to the climatic or behavioural correlates of any differences in life history observed between cooperative and non-cooperative species. Following Russell (1989) and others (Brown 1974, 1987; Gaston 1978; Dow 1980; Ford *et al.* 1988), we looked for associations between mortality and adult dispersal, two measures of climatic variation and latitude. Adult dispersal was characterized in an index of year-round occupancy of a site: 0, sedentary (population does not move far from breeding grounds at any time of the year); 1, part migrant (part of population is migratory, part is sedentary); 2, migrant

(whole population is migratory); 3, nomadic (moves sporadically to find suitable breeding and feeding grounds). Our two indices of climatic variation in the breeding range were a coefficient of annual rainfall variation ((highest value of mean annual rainfall (millimetres) − lowest value of mean annual rainfall across the range of a species)/ mean annual rainfall across the range of a species); and a coefficient of mean annual temperature variation ((highest mean annual temperature (centigrade) − lowest mean annual temperature across the range of a species)/ mean annual temperature across the range of a species). Also, as the range size (maximum degrees longitude of a species range − minimum degrees longitude and maximum degrees latitude of a species range − minimum degrees latitude) could confound climate variables, a multiple regression was done, correlating evolutionarily independent changes in annual mortality with the climate variables while controlling for changes in maximum latitude and longitude range of a species. We were unable to control for altitudinal effects owing to the paucity of data. Finally, latitude was measured as the absolute mean degrees from the equator of a species' range.

The CAIC program was again used to identify and calculate evolutionarily independent contrasts. In these analyses the rate of annual mortality among adults was the dependent variable and the selected extrinsic variables were independent variables. As annual mortality is a continuous variable, the CRUNCH algorithm was used throughout. Two-tailed Wilcoxon signed-rank tests were again used to test for associations between changes in mortality and changes in the extrinsic variables.

3. RESULTS

Cooperatively breeding species are not randomly distributed among avian families. There are eight families that contain significantly more cooperatively breeding species than expected by chance. These families are the Australo-Papuan babblers (Pomatostomidae), the fairy wrens (Maluridae), the anis (Crotophagidae), the bee-eaters (Meropidae), the scrubwrens and thornbills (Pardalotidae), the honeyeaters (Meliphagidae), the treecreepers (Climacteridae) and the corvids (Corvidae) (see table 1). Of these four over-cooperative families, the Australo-Papuan babblers, fairy wrens, scrubwrens and thornbills, and honeyeaters, are exclusive to Australasia. A further 24 families contain twice as many cooperatively breeding species as would be expected by chance (see table 1). However, in many cases the size of the family is so small that this proportion is shown to be not statistically significant when using the binomial test with multiple comparisons. A total of five families contain significantly fewer cooperatively breeding species than expected by chance. These families are parrots (Psittacidae; total number of species $N = 358$; number of cooperative species $k = 1$; binomial probability $R = 1.07 \times 10^{-4}$); hummingbirds (Trochiilidae; $N = 319$, $k = 0$, $R = 3.23 \times 10^{-9}$); pigeons (Collumbidae; $N = 310$, $k = 0$, $R = 4.31 \times 10^{-5}$); tyrant flycatchers and allies (Tyrannidae; $N = 537$, $k = 3$, $R = 3.798 \times 10^{-4}$) and finches and allies (Fringillidae; $N = 993$, $k = 15$, $R = 3.79 \times 10^{-4}$). A further 77 families contain no cooperatively breeding species, but again, in these cases the low proportions are not statistically significantly because of the small sizes of the families.

Changes in the frequency of cooperative breeding were significantly positively correlated with decreases in both

Table 1. *Avian families containing more than twice as many cooperative species as expected by chance*

(Binomial probabilities are the chance of the observed number of species being cooperative, given the total number of species in the family and the fact that 3.2% of all species are cooperative. Asterisks denote families that contain significantly more cooperative species than expected by chance, allowing for the fact that there are 139 families and, therefore, 139 independent binomial tests have been done.)

family	number of cooperative species	total number of species	% of species that are cooperative	binomial probability	significance
Pomatostomidae	5	5	100	3.303×10^{-8}	*
Opisthocomidae	1	1	100	0.032	
Maluridae	26	26	100	4.337×10^{-19}	*
Upupidae	2	2	100	0.001	
Struthionidae	1	1	100	0.032	
Anseranitidae	1	1	100	0.032	
Crotophagidae	4	4	100	1.036×10^{-6}	*
Scopidae	1	1	100	0.032	
Climacteridae	4	7	57	3.288×10^{-5}	*
Orthonychidae	1	2	50	0.062	
Bucorvidae	1	2	50	0.062	
Coliidae	3	6	50	0.001	
Aegithalidae	3	8	38	0.002	
Psophiidae	1	3	33	0.090	
Meropidae	8	26	31	9.346×10^{-7}	*
Picarthartidae	1	4	25	0.116	
Acanthisittidae	1	4	25	0.116	
Pardalotidae	15	68	22	2.869×10^{-9}	*
Phoeniculidae	1	5	20	0.140	
Todidae	1	5	20	0.140	
Laniidae	5	30	17	0.002	
Eurylaimidae	2	14	14	0.063	
Meliphagidae	21	182	12	3.506×10^{-7}	*
Sittidae	3	25	12	0.037	
Lybiidae	5	42	12	0.008	
Petroicidae	5	46	11	0.012	
Apodidae	10	99	10	0.001	
Podicepedidae	2	21	10	0.115	
Certhiidae	9	97	9	0.003	
Corvidae	56	647	9	2.428×10^{-11}	*
Musophagidae	2	23	9	0.130	
Alcedinidae	2	24	8	0.138	

annual mortality (figure 1a: two-tailed Wilcoxon signed-ranks test $z = -3.29$, $N = 27$, $p < 0.01$) and clutch size (figure 1b: $z = -2.58$, $N = 44$, $p < 0.01$). The analyses done on the family-typical values of two life history variables showed that increases among families in the proportion of cooperatively breeding species are significantly correlated with decreases in breeder mortality ($z = -2.70$, $N = 61$, $p < 0.01$). However, changes in clutch size are not significantly correlated with changes in the proportions of cooperative breeders in families ($z = -1.25$, $N = 87$, $p > 0.10$). Both of these results are also true for regression analyses on the raw family-typical data (see figure 2).

Finally, decreases in annual mortality were associated with significant increases in sedentariness ($z = -2.23$, $N = 33$, $p < 0.05$) and significant decreases in latitude ($z = -2.66$, $N = 65$, $p < 0.01$). Decreases in annual mortality were correlated with decreases in the coefficient of annual rainfall variation ($z = -2.34$, $N = 63$, $p < 0.02$). Changes in rainfall variation were also significant when changes in longitude range size ($t = 2.34$, $N = 63$, $p < 0.05$) and latitude range size ($t = 2.08$, $N = 63$, $p < 0.05$) were controlled for. Decreases in annual mortality were also correlated with

decreases in the coefficient of annual temperature variation ($z = -2.44$, $N = 56$, $p < 0.02$), even when controlling for changes in longitudinal ($t = 3.25$, $N = 56$, $p < 0.005$) and latitudinal range ($t = 3.04$, $N = 56$, $p < 0.005$).

4. DISCUSSION

Cooperative breeding is not randomly distributed among avian taxa. Our binomial tests confirm suggestions (Russell 1989; Edwards & Naeem 1993; Cockburn 1996; Rowley & Russell 1997) that there is a concentration of cooperatively breeding species within a small number of higher taxa, with the highest concentrations in families belonging to the parvorder Corvida, such as the honeyeaters and fairy wrens. Most modern Corvida are confined to Australasia, indicating that one or two ancient avian lineages gave rise to most of the cooperatively breeding Australian passerines. However, our new analyses also demonstrate that phylogenetic hotspots for cooperative breeding are not restricted to Australasia, or even to the continents derived from Gondwanaland. For example, cooperative breeding is also overrepresented in
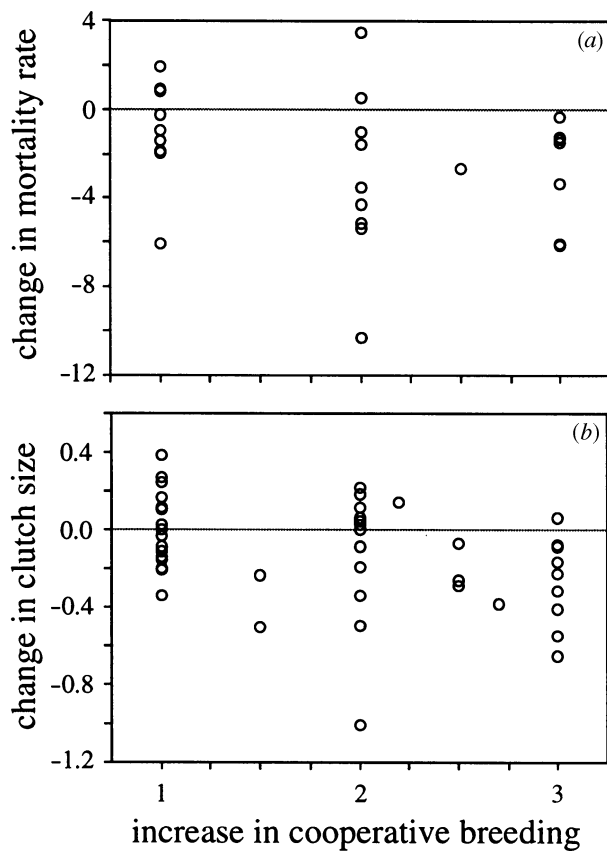
Figure 1. Associations between changes in the frequency of cooperative breeding and changes in: (*a*) annual mortality rate of adults; and (*b*) modal clutch size, controlling for phylogeny. Data points are contrasts resulting from CAIC analysis. Variables are described in detail in the text.

Figure 2. Relations between the proportion of species in a family that are definitely cooperative breeders and the family typical values of: (*a*) annual mortality rate among breeders, $r=0.28$, $p<0.05$; and (*b*) modal clutch size ($r=0.14$, $p>0.10$). Data are raw values. Filled dots represent families excluded from statistical analyses because all species are definitely cooperative breeders.

Eurasian and North American families such as the accentors (Prunellidae) and bush-tits (Aegithalidae) as well as in widespread groups such as the bee-eaters (Meropidae), kingfishers (Alcedinidae) and swifts (Apodidae). The hugely uneven distribution of cooperative breeding does suggest that it may be valid to seek a common biological predisposition to this social system (Russell 1989; Edwards & Naeem 1993; Cockburn 1996). The question now is, was life history variation a key factor in this predisposition?

Our analyses of the power of life history in explaining the pattern of cooperative breeding showed that decreases in annual mortality and clutch size were correlated with significant increases in cooperative breeding. This is interesting because, despite speculation (Heinsohn *et al.* 1990; Cockburn 1996) and a number of tests (Poiani & Jermiin 1994; Poiani & Pagel 1997), this appears to be the first quantitative confirmation of the life history hypothesis. However, this result should initially be treated with caution. From the above analyses alone it is not clear whether cooperative breeding is a cause, or a consequence, of reduced mortality and fecundity. Whereas it is impossible to diagnose the direction of causality unambiguously by using comparative analyses alone, we tackled this problem by performing a family-level analysis to determine whether cooperative breeding is more common in families which display a low rate of mortality, even among species that do not breed cooperatively. A positive
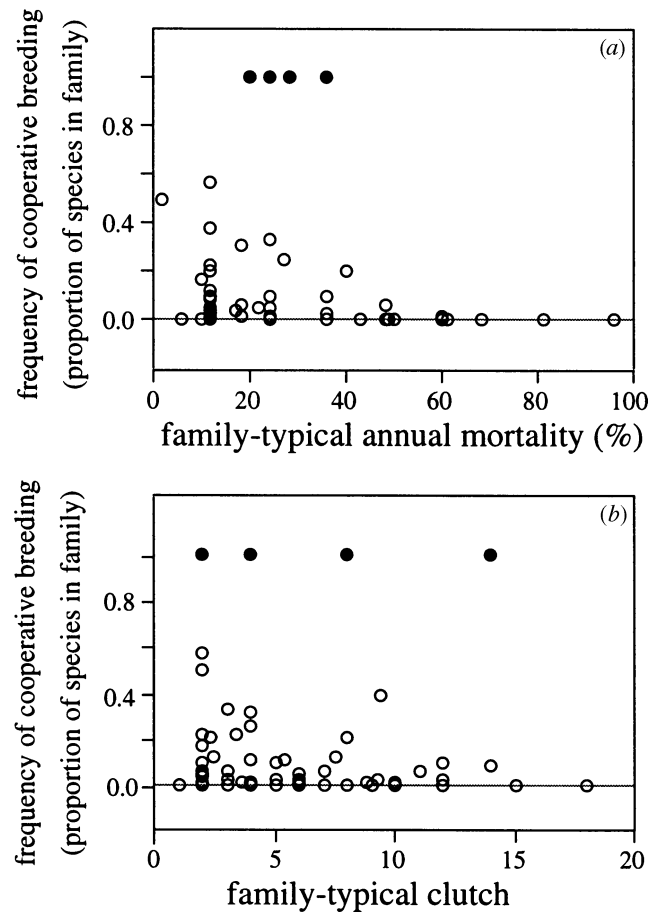
outcome would at least suggest that low rates of mortality predisposed certain avian lineages to cooperative breeding, rather than vice versa. When we did this analysis we indeed found that cooperative breeding is significantly more common in families that have generally high survivorship, suggesting that the relation may be causal. However, no association was found between clutch size and proportion of cooperative breeders per family. These results suggest that decreased rates of mortality have played a role in predisposing certain lineages to cooperative breeding, but that cooperative breeding itself has subsequently led to further decreases in the rate of mortality, and, in particular, a reduction in clutch size.

In our final analysis we looked for extrinsic correlates of life history variation that may facilitate cooperative breeding in certain groups. We found that high breeder survivorship is significantly correlated with living nearer the equator where the temperature and rainfall ranges are less variable, and where territories can be held all year round. This was true even when we controlled for differences in geographic range size, although analyses based on better environmental variation would be interesting.

In summary, our results strongly support the life history hypothesis and we suggest that, like other avian mating

systems (Owens & Bennett 1997), cooperative breeding is a two-step process: a combination of life history predisposition and ecological facilitation. First, a slow life history predisposes certain families to cooperative breeding, because low mortality leads to low population turnover and decreased opportunities for independent breeding. Second, living in a relatively unvariable climate facilitates year-round occupation of territories. Low population turnover combined with reduced dispersal leads to an over-crowded breeding environment. Hence, the breeding habitat is saturated, not owing to any particular feature of the breeding ecology of the species itself, but because the local population turnover is so slow.

However, our evolutionary scenario suggests several questions. First, why does cooperative breeding not occur in other species that belong to long-lived families and inhabit the types of environments that we have identified as conducive to the evolution of cooperative breeding? For example, the eclectus parrot (*Eclectus roratus*) is, surprisingly, the only member of the Psittaciformes reported to breed cooperatively (Heinsohn *et al.* 1997). We suggest that this lack of cooperative breeding in certain long-lived groups is explained by the inability of individuals to maintain year-round territories. For example, parrots' diets of fruit and seeds may force many of them to be locally nomadic (see, for example, Forshaw 1989).

Another question is whether there are alternative pathways to cooperative breeding other than the one we have described here. This does seem likely. For example, the long-tailed tit (*Aegithalos caudatus*) is extremely short-lived and does not have year-round territories, yet it frequently displays cooperative breeding (see, for example, Gaston 1973; Hatchwell & Russell 1996). This sort of observation highlights the fact that the term 'cooperative breeding' is used to describe a massive range of social systems (see, for example, Hartley & Davies 1994), ranging from a monogamous pair of breeders aided by non-reproductive helpers (classic cooperative monogamy) through to polygynandrous co-breeding by members of both sexes (see, for example, Whittingham *et al.* 1997).

5. CONCLUSION

This is, we believe, the first quantitative support for the link between life history and cooperative breeding, and raises a number of further questions. First, how do the evolutionary routes to cooperative polygamy and cooperative monogamy differ? We suggest that life history predisposition may be more important in the classic cooperatively monogamous species than in cooperatively polygamous species (K. E. Arnold & I. P. F. Owens, unpublished data). Second, why do helpers provide different types of care in different species, including predator detection, chick feeding and territory defence? Finally, are there different evolutionary routes to these various forms of mating system that, until recently, have all been put under the behaviourally defined category of cooperative breeding?

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