

Cooperative breeding in oscine passerines: does sociality inhibit speciation?

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Cooperative breeding in birds is much more prevalent than has been previously realized, occurring in 18.5% of oscine passerines known to have biparental care, and is the predominant social system of some ancient oscine clades. Cooperation is distributed unevenly in clades that contain both cooperative and pair breeders, and is usually confined to a few related genera in which it can be ubiquitous. Cooperative clades are species poor compared with pair-breeding clades, because pair breeders evolve migratory habits, speciate on oceanic islands and are more likely to have distributions spread across more than one biogeographic region. These differences reflect the increased capacity for colonization by pair breeders because their young disperse. Thus cooperative breeding has macroevolutionary consequences by restricting rates of speciation and macroecological implications by influencing the assembly of island and migrant faunas.

Keywords: cooperative breeding; oscine passerines; speciation; dispersal; migration; island endemics

1. INTRODUCTION

The incidence of cooperative breeding in birds differs by more than an order of magnitude between different regions, being particularly common in Australia and rare in the Holarctic (Grimes 1976; Rowley 1976; Zahavi 1976; Brown 1987). Ecological factors have been thought to underlie this variation (Brown 1987), but correlates of regional differences have remained elusive. For example, various authors have interpreted the high incidence of cooperative breeding in the Australian avifauna as having no environmental correlates, or as resulting from unpredictability, aseasonality or predictable seasonality (reviewed by Cockburn 1996). The inability to identify environmental correlates is a problem for the ecological-constraints hypothesis, which argues that cooperative breeding occurs because dispersal is impossible owing to a shortage of territories or mates (habitat saturation), or when the value of the current territory to the philopatric young is greater than any alternative (benefits of philopatry). While it is possible to identify constraints operating on individual cooperative breeders, it has not proved possible to predict when species will adopt natal philopatry instead of alternative solutions to constraint such as floating (Koenig *et al.* 1992). Indeed, nobody has offered a definition of 'constraint' or 'saturation' that can be applied in any predictive sense (Cockburn 1996, 1998; Hatchwell & Komdeur 2000; Kokko & Lundberg 2001; Kokko & Ekman 2002), as most birds are expected to face constraints.

More recently it has been shown that the incidence of cooperative breeding also differs dramatically between clades of birds (Russell 1989). For example, most cooperative breeders belong to an immense cosmopolitan radiation, the oscine passerines. DNA hybridization has suggested that the oscines fall into two groups: the Corvida, which clearly originated in Australia but also dispersed elsewhere, and the Passerida, where Australian representatives were derived from Eurasian ancestors. Russell (1989) showed that *ca.* 25% of Australian Corvida breed

cooperatively, while no Australian passerid does so. She suggested that prolonged exposure to ancient features of the Australian environment could cause a propensity to breed cooperatively. However, when the data were corrected for our comparatively poor knowledge of the avifaunas of tropical Africa, Asia and the Americas, Cockburn (1996) showed that the incidence of cooperative breeding in the Corvida is about the same in all avifaunal regions.

Such phylogenetic biases lend support to the life-history hypothesis, which argues that this phylogenetic inertia in social habits might reflect the way that the life histories of taxa are organized, and hence social organization might be retained in taxa despite differences in ecology. In particular, slow life histories with low clutch sizes and high survival promote cooperative breeding. This idea has attracted interest from theoreticians (Pen & Weissing 2000; Kokko & Lundberg 2001; Kokko & Ekman 2002; Hårdling & Kokko 2003; Ridley & Sutherland 2002) and has been further stimulated by comparative analyses by Arnold & Owens (1998, 1999) who, in a widely cited result, showed that the incidence of cooperative breeding in clades of birds is not associated with ecological factors or the clutch size prevalent in the clade, but increases with clade-level estimates of adult survival.

Unfortunately, there are reasons to treat this apparent support for the life-history hypothesis with caution. First, theory predicts cooperative breeding in any sedentary long-lived bird, but most such species do not breed cooperatively. Therefore, as for the ecological-constraints model, the problem becomes to explain the absence of cooperative breeding rather than its presence. Second, comparative data for the Passerida and Corvida are not of equal quality. Cockburn's (1996) data were used for the Corvida, and were based on an assessment of each species to determine whether they were cooperative or pair breeders, they had some other system of parental care, or the pattern of parental care was unknown. By contrast, assessments of prevalence in the Passerida assumed that any species not listed in Brown's (1987) review is a pair

breeder. However, we can confidently assign the pattern of parental care in even fewer members of the Passerida than the Corvida. For example, Isler & Isler (1999) reviewed the breeding biology of 256 species of thraupine tanagers and reported evidence of cooperative breeding in 11 (4.3%) of these. However, there are just 52 species (20%) with data on nestling care, suggesting an incidence of 11 out of 52 (21%). Third, Arnold & Owens' results are surprising because they report different predictive abilities for clutch size and survival, but all comparative studies suggest that these life-history traits are highly negatively correlated, so each should have equivalent predictive power (Martin 1995; Martin *et al.* 2000; Bennett & Owens 2002). Although there have been theoretical attempts to explain this discrepancy (Hårdling & Kokko 2003), the positive correlation between cooperative breeding and survival is worrying because the life-history data used to characterize the clades of birds were of uneven quality. Data on clutch size were available for 2458 species, but data on survival were available for only 264 species (Bennett & Owens 2002). The final difficulty is that refinement of the avian phylogeny shows that one of the original arguments underlying the life-history hypothesis is wrong. We now believe that the Corvida as originally recognized includes the Passerida, which branched from the old Australian stock only after several major taxa had emerged and radiated in Australia (Barker *et al.* 2002; Ericson *et al.* 2002). Thus all oscines have Australian origins, and the Passerida and Corvida share a common reproductive and ecological past.

Prompted by these difficulties, I present a new data compilation and analysis of the distribution of cooperative breeding in all oscines, and interpret the patterns in the light of the new phylogenetic hypothesis. My analyses explain many of the previous inconsistencies, and suggest hitherto undetected patterns in the distribution of sociality. In particular, I conclude that much of the relative prevalence of pair and cooperative breeding is explained by lower rates of speciation among cooperative breeders, which in turn results from the restrictions that philopatry places on the colonization of new habitats.

2. METHODS

(a) *Literature sources*

Although my starting point was the existing reviews of the distribution of cooperative breeding (Grimes 1976; Rowley 1976; Zahavi 1976; Brown 1987; Skutch 1987), I updated these compilations by seeking accounts of breeding behaviour in all the recent monographs covering taxonomic groups or regional avifaunas. Where the behaviour of a species could be characterized from these secondary sources, I cite them in table 2 in electronic Appendix A, available on The Royal Society's Publications Web site. However, in some cases, I referred to the original literature to make my decision, and have cited the older source accordingly. For all species not covered in recent monographs, I used the 'Zoological Record' to determine all relevant literature published since 1978. I conducted additional literature searches in 'Zoological Record' and 'Web of Science' using the terms 'cooperate', 'co-operate' and 'help'. Finally, I contacted ornithologists working on particular species for which published data were unavailable or contradictory.

(b) *Types of parental care*

I recognized seven classes of parental care. Brood parasitism occurs where care is provided by other species. Uniparental care occurs in lekking species, in some cases of extreme polygyny and in a number of unusual societies. Pair breeding was assigned to any species where there was evidence of living in pairs during the breeding season and that both sexes feed the young. Cooperative breeding was assigned where a reasonable proportion of broods in at least one population are provisioned by more than two individuals. In some species, there are good grounds to conclude that cooperative breeding is likely (e.g. taxa that occur in groups throughout the breeding season and where supernumerary birds feed fledglings but where there are no observations of care of nestlings). These birds are classified as 'suspected', and are included in the analyses as true cooperative breeders. By contrast, in many species additional provisioning has been reported, but occurs with negligible frequency, most often when parents have lost their own nest but are still hormonally primed to respond to begging (to the extent that they will often provision young of different species). I classified these species as 'occasional' cooperative breeders, but treat them as pair breeders in the analyses. Owing to the incompleteness of the literature, it was not possible to use a single definition that distinguished between occasional and cooperative, though in general in cooperative species helpers attend more than 10% of nests.

In cases where different populations exhibited different behaviours, I assigned the highest category of complexity to the species. For example, cooperative behaviour occurs commonly in Spanish populations of the carrion crow *Corvus corone* (Baglione *et al.* 2002), so it is classified here as a cooperative breeder. By contrast, some level of helping or joint-nesting has been recorded repeatedly in blue tits, *Parus caeruleus*, but it is nowhere frequent. Hence, this species is classified as occasional.

However, in many cases, it was impossible to derive reliable conclusions, so the species was classified as 'unknown'. The most common reason for deciding that the social system was unknown was where there were no observations of nesting, let alone parental care. I was particularly conservative in assigning a mode of parental care where data were confined to observations of just a few nests but where complex mating systems were known from more detailed studies of close relatives. For example, the three intensively studied accentors (*Prunella* spp.) have complex polygynandrous societies (Davies 1992), so I have assumed that the skeletal data on other species are insufficient to preclude the possibility that complex systems are universal. I was also conservative in genera where there are data on only a single species. Last, I identified seven species where birds live in cohesive territorial groups during the breeding season but only the dominant pair provision the young during the nestling phase, though in some it is clear that supernumeraries contribute to provisioning or to nest defence when the young fledge (Waite & Strickland 1997; Nakamura *et al.* 2001). For the analyses, I treat these birds as unknown, as the observations required to confirm this type of cooperative breeding have only rarely been obtained.

(c) *Movement*

I distinguished species that were mobile because of migration or nomadism from those that were resident year-round, and identified species that were endemic to small oceanic islands.

(d) *Phylogeny*

Following Barker *et al.* (2002), I recognize three major groups among the oscines: the core Corvoidea (including Petroicidae and Melanocharitidae), the Passerida (including Picathartidae) and the old Australian clades that diverged before the split into these major groups. Within these radiations I generally used the taxa recognized by Sibley & Monroe (1990, 1993) as tribes, or, where subfamilies or families were not divided into tribes, the higher categories. An exhaustive reinterpretation of the systematics was not attempted, so I followed Sibley & Monroe (1990, 1993) in assigning species to clades, except in several potentially informative cases where there was convincing evidence for reassignment (see electronic Appendix A).

In addition to the well-supported changes, there is growing evidence that Sibley & Monroe's (1990, 1993) classification is deficient with respect to taxon boundaries within the huge fringillid radiation, where many genera and higher taxa are paraphyletic and polyphyletic (e.g. Burns 1997; Groth 1998; Klicka *et al.* 2000; Loughheed *et al.* 2000; Yuri & Mindell 2002). Apart from the icterines (see electronic Appendix A) there is no resolution of this problem, so I therefore conducted all analyses at the levels of genus and tribe both including and excluding the fringillid subtaxa except for the icterines. This did not affect the significance of any analysis, but here I report analyses with the fringillids excluded.

3. RESULTS

In the most comprehensive previous compilation, Brown (1987) identified 160 oscines as cooperative breeders (from the 222 cases among all birds). In the light of new information, or reinterpretation of the original sources, I believe that six of these should be reclassified as occasional (*Phylidonyris novaehollandiae*, *Motacilla capensis*, *Thryothorus pleurostictus*, *Erithacus rubecula*, *Cardinalis cardinalis* and *Hirundo rustica*), one as 'pair' (*Philemon citreogularis*) and one as 'uniparental' (*Orthonyx temmincki*), leaving 152 oscines as cooperative breeders (3.3% of 4583 species). I found accounts of cooperative breeding in an additional 153 species, and evidence of suspected cooperative breeding in a further 78, bringing the total to 383 species (8.4%). However, a further 22 species were brood parasites, 109 had uniparental care and 2385 were unknown. Thus, out of 2067 species known to exhibit biparental care, 18.5% breed cooperatively. Out of the 1684 species that I will analyse here as pair breeders, helping behaviour has been recorded occasionally in 62 (3.7%).

There are 90 taxa of tribe or above recognized by Sibley & Monroe (1990, 1993) or requiring distinction because of recent phylogenetic studies. The viduine finches are brood parasitic and five taxa are largely uniparental (Altrichothorminae, cnemophilines, Menurinae, Parasidaeni and Ptilonorhynchidae). It was difficult to draw conclusions about the habits of 12 taxa because the data were too few (Aegithininae, *Chloropsis*, Drepanidini, Dulini, Falcunculini, Melanocharitidae, Paramythiidae, Pardalotinae and Picathartidae) or their habits are difficult to classify (Aegithalidae, Garrulacinae and Orthonychidae). For example, Zahavi's (1976) compilation included a table co-authored with A. J. Gaston, who suggested that all 54 species of *Garrulax* (Garrulacinae) are cooperative breeders. Gaston was familiar with cooperative timaliine

babblers (*Turdoides*) and considered *Garrulax* identical. Similarly, Ali (1981) called the characteristic foraging groups of both genera sisterhoods. However, Brown (1987) did not attribute cooperation to any *Garrulax*, no doubt because there were no published studies confirming cooperation. My own literature search uncovered descriptions of joint territory defence (Sheldon *et al.* 2001), joint nest building (Banks & Banks 1987; Zacharias 1997), joint nest defence (Roberts 1992) and helping behaviour in large aviaries (Young 1978; Haines 1989; Mace 1991), but the only detailed field observations of parental care report pair breeding (Islam 1994, 1995). It seems certain that the genus exhibits both habits, and it may rival *Turdoides* as the genus containing the greatest number of cooperative breeders. However, the true frequency of cooperation remains unknown.

Out of the remaining 72 clades, eight are 100% cooperative, though six of these comprise just a single genus; 38 are largely pair breeders (generally more than 90% of species with biparental care breed as pairs), with 14 comprising a single genus (table 3 in electronic Appendix B); and 26 are 'mixed', including representation of both habits (see table 4 in electronic Appendix B). I used binomial models with a logit link to evaluate whether cooperative breeding was distributed randomly among genera within the mixed clades. Models were fitted with the number of cooperative breeders in each genus as the response variable and the number of cooperators and pair breeders combined as the number of cases. Models contained no explanatory terms, and departure from binomiality was assessed using the deviance associated with the error term as the test where the degrees of freedom = (number of genera - 1). In the Cisticolidae, cooperation was randomly distributed among genera (see table 4 in electronic Appendix B). However, cooperative breeding was not randomly distributed among genera in 20 clades (see table 4 in electronic Appendix B). The same tended to be true for an additional five clades ($p < 0.10$).

Further inspection revealed that the cooperative genera are typically clustered together in systematic sequences, and are often the outgroup to the pair breeders (see electronic Appendix A). The following examples are illustrative: (i) the Troglodytinae (New World wrens) have 10 genera and 34 species for which data on social behaviour are available—the first two genera in the usual systematic sequence (*Donacobius* and *Campylorhynchus*) are exclusively cooperative, while the eight remaining genera for which there are good data breed exclusively as pairs; (ii) in the Laniidae (true shrikes) there are two small exclusively cooperative genera (*Corvinella* and *Eurocephalus*), which are outgroups to one larger genus that contains cooperative breeders but is largely pair breeding; and (iii) in the Monarchini, two cooperative African genera (*Erythrocercus* and *Elminia*) are probably an outgroup to the remainder of the clade, in which cooperative breeding is known only from one island endemic (*Pomarea dimidiata*).

The presence of cooperative clusters within clades and of exclusively cooperative clades indicates that cooperative groups are often ancient, allowing comparison between 'pair' and 'cooperative' radiations. Unfortunately rigorous phylogenies are unavailable for most of the taxa. To develop hypotheses that might prompt interest by systematists in these questions, I initially examined patterns of

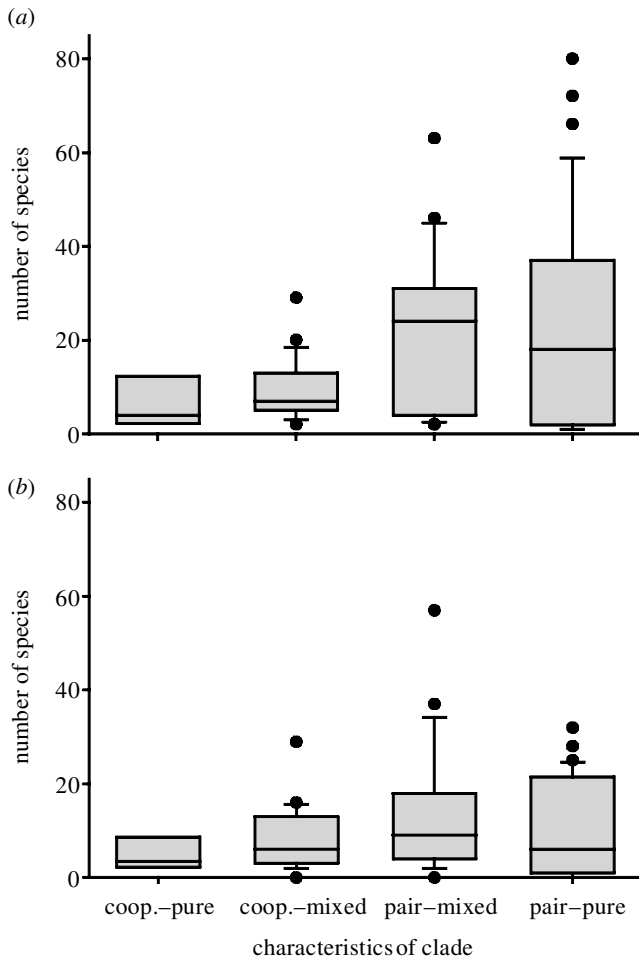


Figure 1. The numbers of species in the largest cooperative and pair-breeding genera in oscine passerine clades that are dominated by one form of parental care (pure) and clades that contain both habits (mixed). (a) All species in the genus and (b) all species that are not migratory, nomadic or resident on small oceanic islands. The box plots depict the tenth, 25th, 50th, 75th and 90th percentiles in the data. Points below the tenth and above the 90th percentiles are shown.

diversification using a pairwise analysis. I determined the most speciose pair- and cooperative-breeding genus in each clade (table 4 in electronic Appendix B). In the mixed clades with both habits, pair-breeding genera contain more species than their cooperative counterparts (paired t -test: $t = 3.2$, d.f. = 22, $p = 0.004$; figure 1a). Genera from the purely cooperative or pair-breeding clades have similar species richness to the genera from mixed clades with the same pattern of parental care (figure 1a). Overall, pair-breeding clades are more species rich (with species richness square-root transformed to improve the distribution of residuals: $F_{1,94} = 7.6$, $p = 0.007$; figure 1a).

This difference in species richness is caused by three effects. First, species-rich pair-breeding genera contain large numbers of mobile species, while cooperative genera are comprised largely of residents (tables 3 and 4 in electronic Appendix B), in which movement is confined to intra-continental movements such as seasonal nomadism or short-distance altitudinal migration. Second, pair-breeding clades often include endemics on small oceanic islands (tables 3 and 4 in electronic Appendix B). By con-

trast, the only two cooperative clades with several such endemics are the Galápagos mockingbirds *Nesomimus*, which have presumably evolved cooperative habits *in situ*, and the poorly studied woodswallows *Artamus*. When only resident birds are considered, cooperative and pair-breeding genera have similar species richness (figure 1b; mixed clades, Paired: $t = 1.5$, d.f. = 22, $p = 0.14$; all clades with data square-root transformed: $F_{1,94} = 0.03$, $p = 0.86$). Third, there are 17 genera that have 20 or more species despite the removal of migrants and island endemics, but only two of these are restricted to a single zoogeographical region (*Tangara* and *Thryothorus*), indicating that diversity among resident species itself depends on dispersal between landmasses. Only one out of the remaining 15 genera is cooperative (*Turdoides*), and it is unique among the 17 genera in having a continuous distribution across the deserts that intervene between its two centres of diversity in Africa and southeast Asia.

4. DISCUSSION

Cooperative breeding is now known in 8% of oscine passerines. However, when species with unknown patterns of provisioning are excluded, the incidence rises to 13%. Excluding brood parasites and species with uniparental care reveals that 19% of the oscine passerines that are known to have biparental care breed cooperatively. There are several problems with assuming that the unknowns have parental-care systems in proportion to the species that have been studied. For example, the most comprehensive data are for palaeartic and nearctic migrants, but the migratory habit has been consistently associated with a low level of cooperative breeding. Alternatively, high-quality studies of parental care may reflect 'cherry-picking', and be biased towards species with unusual social systems. Nonetheless, it is obvious that the incidence of cooperative breeding has been substantially underestimated.

The data support my earlier findings that cooperative breeding is most common among the older branches of the oscine radiation, and is often ubiquitous in those branches (Cockburn 1996). Cooperative breeding was more prevalent among the old Australian groups (79 out of 155 species with biparental care; 51%) than either the Corvoidea (99 out of 355; 28%) or the Passerida (205 out of 1557; 13%), although the frequency in the Passerida is considerably higher than has been recognized. Among the old Australian taxa, the only groups that do not include cooperative breeders are very small (*Dasyornithinae*) or exhibit uniparental care. However, exclusive pair breeding occurs in large clades within the Corvoidea (*Rhipidurini* and *Vireonidae*) and Passerida (*Motacillinae*, *Estrildinae* and *Carduelini*).

(a) *Patterns of diversification*

Among the large taxa exhibiting both cooperation and pair breeding, cooperation was heterogeneously distributed between genera. Despite this, cooperative radiations appear to be species poor compared with their pair-breeding counterparts. The driving reason for this difference is that a large part of the species richness of pair breeders comprises species exhibiting habits not found among cooperative breeders: migration, and endemism on small

Table 1. The distribution of clades of oscine passerines with different patterns of parental care in Melanesia. Numbers in parentheses refer to the number of species in Melanesia/number in northeast New Guinea. Distribution data are from Mayr & Diamond (2002), adjusted to correct a number of minor errors in their classification. The five species of Cinclosomatinae are excluded as the habits of the New Guinean species is too poorly known to allow categorization of parental care. The three mixed taxa below the line contain only pair taxa in New Guinea.

	cooperative	mixed	pair
no occupancy of islands	Maluridae (0/5) Pomatostomidae (0/1) Neosittini (0/1) Orthonychidae (0/1)	Oriolini (0/1) Laniidae (0/1) Climacteridae (0/1)	Motacillinae (0/2) Alaudidae (0/1)
occupancy of islands by pair species only		Monarchini (8/10) Acanthizini (1/16) Petroicidae (2/21) Pachycephalini (3/22)	
		Sylviidae (4/8) Corvini (2/2) Sturnini (6/4)	
occupancy of islands	Artamini (1/6)		Rhipidurini (6/10) Estrildinae (3/9) Dicaeini (1/8) Campephagini (1/2) Dicurini (1/2) Zosteropidae (7/4) Hirundinidae (1/1) Nectariniini (2/2) Turdinae (3/5)

islands. Much of the remaining difference occurs because pair breeders are more likely to spread between biogeographical regions.

The absence of island endemics from cooperative genera was unanticipated because some of the most famous cooperatively breeding species occur on islands (Curry & Grant 1990; Komdeur 1992). However, such species are derived from taxa that are primarily pair breeders, and the secondary derivation of cooperative breeding has sometimes been confirmed by phylogenetic analysis (Leisler *et al.* 2002). This suggests that mainland cooperative breeders cannot colonize islands. Strong support for this interpretation comes from reanalysis of the remarkable work by Mayr & Diamond (2002) on the distribution of birds in Melanesia. In a recent synthesis, they classified the capacity of the avifauna of northern New Guinea to disperse successfully across the short distances required to occupy the Melanesian islands. They identified some taxa as poor colonists and others as good dispersers. However, the explanation they proffered for the variation in vagility was differences in the ability to fly. There is no independent measurement of capacity for long-distance flight that supports this assertion. However, I have reanalysed these taxa in relation to social system and revealed an excellent negative correlation between cooperative breeding and dispersal ability (table 1). Out of five exclusively cooperative clades in northern New Guinea, only one (Artamini) has a species that has spread into Melanesia. By contrast, nine out of 11 exclusively pair-breeding clades have dispersed successfully, and the remainder are largely African clades for which New Guinea is near the edge of their distribution. Out of 10 clades that comprise both pair-breeding and cooperative genera, eight have colonized successfully, always via pair breeders.

These island data provide a new perspective on the well-known negative association between migration and cooperation, traditionally interpreted to result both from the inability of migrants to retain their territories and hence the lowered probability of kin association that could foster cooperative breeding. However, the phylogenetic evidence suggests that exactly the opposite could also be true: cooperative species may be successful in their area of origin but are unlikely to evolve the capacity to migrate. Thus the low diversity and limited geographical spread of cooperative breeders may have a general cause. Because at least one sex in cooperative breeders is frequently completely philopatric, colonization of new habitats is rare, precluding occupancy of islands, movement between landmasses and expansion into habitats suitable for seasonal exploitation by migrants. By contrast, I hypothesize that both sexes of the young of pair breeders are forced to disperse, often leading to long-distance colonization and, occasionally, to speciation and radiation. Although the species richness of a clade will reflect a balance between extinction and speciation, speciation alone seems most important in generating the patterns, as the species richnesses of cooperative and pair-breeding taxa are almost identical once the 'colonist' species have been removed (figure 1*b*), and some of the habits of pair breeders (island endemism and colonization of temporarily available migratory grounds) predispose them to extinction.

Numerous additional observations support the idea that cooperation constrains colonization. First, while population expansion of birds is facilitated by the occasional successful dispersal of vagrants (Veit 2000), population expansion in some cooperative breeders is confined to fission of groups at the margins of the existing range (Williams *et al.* 1994). Second, disjunct distributions in

cooperative breeders are non-existent or best explained by fragmentation of once-continuous populations (Fok *et al.* 2002). Third, such fragmentary populations can persist on small islands created by rising sea levels (Driskell *et al.* 2002), suggesting that colonization rather than persistence limits distribution.

These observations suggest the surprising result that the adoption of a trait such as cooperative breeding that has evolved and been lost many times may have profound macroevolutionary and macroecological consequences. First, the higher rates of dispersal lead to a greater speciation rate in pair-breeding clades, generating the prediction that pair breeding will be more prevalent as a result of this effect alone. Second, the assembly of communities may reflect the social habits of their colonist ancestors. While autochthonous radiations in the continent of origin can consist of cooperative breeders, allochthonous faunas generated by dispersal will be composed of birds whose ancestors bred as unassisted pairs.

(b) *Previous comparative analysis*

These macroevolutionary and macroecological consequences cast previous comparative analyses into a new light. Russell's (1989) observation that the Passerida in Australia do not breed cooperatively need not indicate that passerids are intrinsically unlikely to do so. Instead, those passerids that have managed to disperse back over Wallace's line are likely to be derived from good colonists, and hence pair breeders. Supporting this assertion, the Australian passerids are derived from some of the clades least likely to breed cooperatively (estrildines, alaudids and motacillines), while highly cooperative taxa in southeast Asia such as timaline babblers have failed to reach Australia.

My interpretation also allows reinterpretation of the puzzling result of Arnold & Owens (1998), who found that the incidence of cooperation in families is correlated with the average level of survivorship in families, but not with clutch size. I argue that the result for survivorship is an artefact. Because there was an order of magnitude more data for clutch size than for survivorship, characterization of 'family' values for survival data will be much more susceptible to the effects of sampling only a small fraction of the habits exhibited by particular families. I. P. F. Owens (personal communication) has kindly provided me with the original dataset, and, while the clutch-size data were comprehensive, it is clear that the survival data were biased. Southern Hemisphere cooperative breeders and holarctic species that breed as unassisted pairs at high latitudes were well represented, while the species with the modal habit (tropical or Southern Hemisphere residents breeding as pairs) were badly underrepresented. Arnold & Owens (1998) had data for just eight such species in their sample of 119 oscines. However, out of 2058 African, Australian and central- and south-American species in my dataset, 968 were year-round residents that bred as unassisted pairs. Increased clutch size and reduced survival with increased latitude is the most robust life-history trend in passerines (Lack 1968), and I contend that the patterns reported by Arnold & Owens (1998) confound the transition between cooperative and pair breeding with the transition to the 'fast' life histories associated with breeding at high latitudes, particularly among migrants.

To gain better evidence of a causal effect it is necessary to control for the effects of latitude and migration. Indeed, because cooperative breeders often co-occur with pair-breeding relatives, I was able to identify 24 clades where it was possible to compare the clutch sizes of cooperative breeders and their pair-breeding relatives from comparable geographical regions and latitudes. Like Arnold & Owens (1998), I found no support for the idea that cooperative and pair breeders differ in clutch size (mean increase in cooperative breeders relative to their pair-breeding relatives = 0.06 ± 0.11 s.e.; paired *t*-test = 0.52, d.f. = 23, $p = 0.61$). Contrasts in survivorship remain moot because the data are inadequate, a problem unlikely to be resolved until we have more studies of the survival of pair-breeding tropical residents. However, I predict that appropriate analysis will not reveal informative differences, as it will mirror the pattern suggested by clutch size. Indeed, anecdotal data support the view that pair-breeding tropical species can be exceptionally long lived, and the few available carefully controlled contrasts suggest that pair breeders may have slightly higher survival (Atwood *et al.* 1990; Noske 1991; Green & Cockburn 1999).

This analysis suggests that a full understanding of the relative prevalence of cooperative and pair breeding requires solutions to three quite distinct questions.

- (i) Why do some clades develop early in their history into separate groups that thereafter persist in cooperative or pair breeding?
- (ii) Why do taxa that are committed to pair and cooperative breeding differ in their extent of diversification?
- (iii) Why do non-cooperative groups occasionally develop cooperative breeding, particularly on islands?

The answer to the first question may require new theory. This paper offers a solution to the second question, but confirmation of my hypothesis requires rigorous phylogenies for many taxa that have thus far escaped the attention of molecular systematists. The evolution of cooperative breeding on islands, in otherwise non-cooperative taxa, is consistent with both ecological-constraints and life-history models. Although this is probably the strongest evidence that such models can predict interspecific differences, ecological models may have limited potential to explain the overall distribution of cooperative breeding.

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