

Cooperate or speciate: new theory for the distribution of passerine birds

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In cooperatively breeding birds, adults often forego reproduction and help care for the offspring of others. A universal explanation for this mode of breeding has eluded evolutionary biologists, who have considered it to be a rare, and largely Australian, phenomenon. In a recent paper, Andrew Cockburn reports that the number of known cooperative breeders among oscine passerine birds has more than doubled since the last substantial review, published 16 years ago. Cooperative breeding is often the ancestral trait, and predominantly cooperative genera are species poor compared with their pair-breeding counterparts. Cockburn argues that speciation is less likely in cooperative clades, because the philopatric tendencies of individuals make them poor dispersers, colonizers and migrants. This new hypothesis helps explain the distribution and composition of migrant and island avifauna. However, a major challenge remains to reconcile the roles of phylogenetic history and current ecology in promoting cooperative behaviour.

Why some adult birds assist the breeding attempts of others and forego breeding themselves has been hotly debated for over four decades. Such 'cooperative' breeding behaviour was first described in Australia [1], first studied in Central America [2], and has since been regarded as a rare and 'almost always tropical, subtropical, or Australian' phenomenon [3]. A recent review of cooperatively breeding oscine passerines by Andrew Cockburn [4] confirms that cooperatively breeding birds are scarce at high latitudes, but challenges the 'rare' and 'primarily Australian' labels. He catalogues many newly reported cooperative breeders but recognizes, for the first time, that cooperative species frequently belong to species-poor genera compared with pair-breeding species. This led Cockburn to propose that cooperation inhibits speciation because the philopatric tendencies of cooperative breeders inhibit colonization and migration (i.e. they tend to return to, or stay in their home range). This new hypothesis not only influences our understanding of cooperative breeding, but also of migrant and island assemblages and the global diversity and distribution of passerine birds.

Oscine passerines

The oscine passerines, which includes almost half of the ~10 000 extant avian species, can be separated into two

major groups (the Corvida and Passerida) based on DNA–DNA hybridization data [5] (Figure 1). Although predominantly Australasian, the Corvida occur worldwide [6,7], and show a high propensity for cooperative breeding. The Passerida, although centered in the Old World and North America, are also common worldwide and relatively few species were thought to breed cooperatively [6]. This distribution led to the suggestion that the ancient Australian environment somehow promoted cooperative breeding, leaving the Corvida phylogenetically predisposed towards such behaviour [6,7]. This theory has been dispelled by recent phylogenetic analyses that identified eastern Gondwana (Antarctica and Australasia) as the origin of both the Passerida and Corvida [8,9], and show the latter to be paraphyletic and basal to the Passerida (Figure 1).

How common is cooperative breeding?

Starting with Brown's [10] seminal review, Cockburn conducted extensive literature searches on each oscine

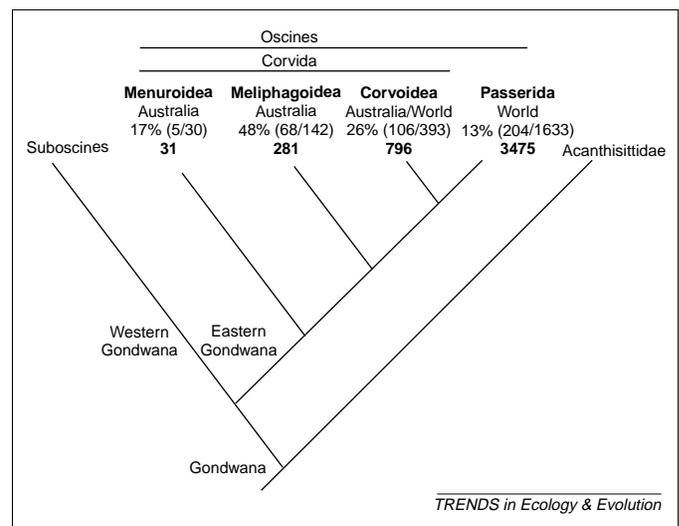


Figure 1. Distribution of cooperatively breeding species among the oscine passerines. The two major clades within the order Passeriformes are the suboscine and oscine passerines. Formerly, the latter has been split further into two parvorders, the Passerida and Corvida. Recently, however, the Passerida clade has been found to be nested within the Corvida [8,9] and thus the Corvida is now considered paraphyletic (i.e. it does not contain all the descendants of the most recent common ancestor). The percentage of cooperatively breeding species only includes taxa that have been adequately studied to categorize their parental behaviour (total in parentheses). The total number of species in each clade is in bold. For simplicity, the Meliphagoidea, Meliphagoidea and Corvoidea are presented as monophyletic, although this has recently been refuted [23]. (After [8]).

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species as well as drawing heavily on recently published, regionally based monographs describing the avifauna of the world. However, the approach taken to classify species as cooperative breeders differed from previous reviews in three ways. First, it was explicitly recognized that information about breeding behaviour is still lacking for many, if not most, avian species, and pair breeding was not assumed in those cases. Second, species with only occasional helping behaviour were categorized as pair breeders. Third, species were recognized as cooperative breeders if they were strongly suspected to be so (e.g. group-living or helpers seen to feed fledglings). A major limitation of the available data and subsequent analyses was the treatment of cooperative breeding as one broad category. There was no attempt to distinguish between types of breeding group, such as helper-at-the-nest systems formed through natal philopatry versus polyandrous groups with unrelated males who share a breeding female, even though the ecological basis for these social systems might differ [11,12].

Definite accounts of cooperative breeding were found in 153 species not identified in previous reviews, and a further 78 species were identified as 'suspected' cooperative breeders. Therefore, in total, 383 (8.4%) of the 4583 species of oscine passerines are now either known, or are strongly suspected, to breed cooperatively (Figure 1). However, the parental behaviour of 2385 oscine species has not been described so the frequency of cooperative breeding could be as high as 17% of species. These percentages probably represent the lower and upper limits of cooperative breeding among oscines, but nonetheless demonstrate that the phenomenon is more frequent than was previously recognized. Its prevalence among other bird groups (e.g. Accipitridae and Falconidae) is also likely to have been underestimated [13].

Examination of the electronic appendix supplied by Cockburn shows that cooperative species within the Passerida now outnumber those found among the other oscine groups combined (204 versus 179) but still account for only 12% of the 1633 species studied in this species-rich clade. (Figure 1). Nearly a third of the now taxonomically defunct (Figure 1) Corvida clade are known to breed

cooperatively (179 out of 565), but, similar to the Passerida, the breeding habits of about half the group remain undescribed. Also the prevalence of cooperatively breeding oscine species has shifted towards Africa (134 species); proportionally, however, the Australasian region, with 115 species, is the world hotspot for cooperatively breeding birds – but only just (11% versus 13% of all endemic oscine species, respectively). By contrast, cooperative breeders in northern temperate regions comprise ~5% of all oscine species.

Does cooperation inhibit speciation?

The distribution of cooperative species among lower taxonomic groups was also non-random. Of 72 well resolved tribes or equivalents, only eight were entirely cooperative, whereas 38 were almost exclusively pair breeders. In the remaining 'mixed' tribes, cooperative genera were usually clumped, were likely to be basal to pair-breeding genera and were likely to contain significantly fewer species. Thus, cooperative breeding appears to be associated with a lower rate of speciation, which could explain Ricklefs' recent observation [14] that Australia is home to many species-poor passerine clades. Cockburn hypothesized that the philopatric tendencies of at least one sex in most cooperatively breeding species render them poor colonizers and migrants. Such species would be less likely to spread to new habitats and might diverge to form new species more slowly.

Cockburn's hypothesis has macroevolutionary implications and could, in part, explain the current distribution and breeding behaviours of many extant birds. When eastern Gondwana collided with the southeast Asian plate (Figure 2) the oscine passerines, and perhaps the more dispersive pair-breeding passerids in particular, radiated north and eventually reached the Americas. By contrast, the under-representation of the other oscine clades outside Australia and among migrant assemblages could reflect their poor dispersal abilities. However, the hypothesis fails to explain the presence of cooperative non-passerid oscines in Africa and would have to invoke a more complicated sequence of lost and regained cooperative

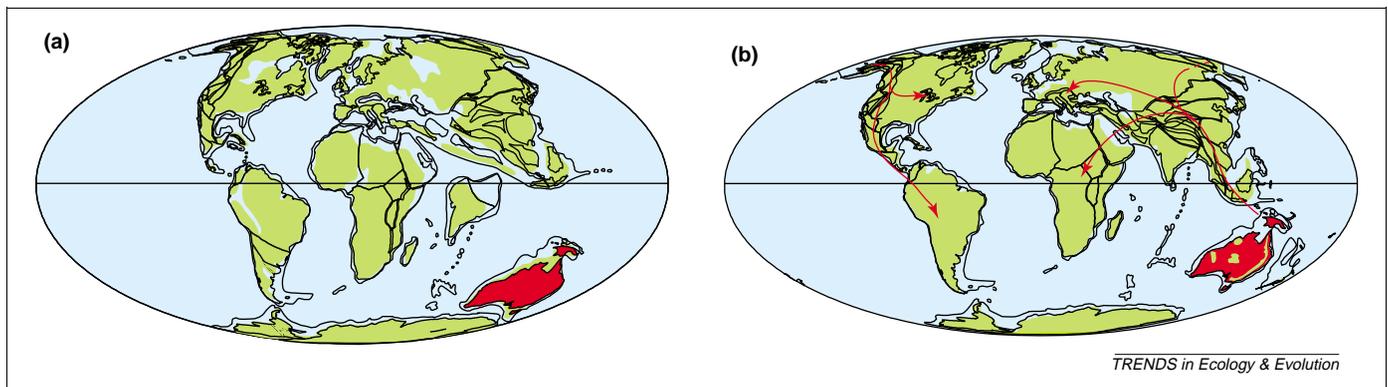


Figure 2. The movement of the Australia/New Guinea plate between 60 (a) and 20 (b) million years ago (Mya). When New Zealand separated from Antarctica ~85 Mya, only South America, Antarctica and Australia/New Guinea remained as the last pieces of the Gondwanan supercontinent. Around 55 Mya, Australia/New Guinea broke away from Antarctica and moved north. When Australia/New Guinea finally collided with southeast Asia ~15 Mya, the oscines (and the ancestors of the Passerida in particular) were able to disperse rapidly into Asia and, from there, reach Africa and the Americas (possible dispersal routes are indicated by arrows) [8,24]. Original palaeogeographic maps courtesy of Chris R. Scotese [25].

behaviours to account for this disjunct distribution. The theory also explains why cooperative island-dwelling species usually belong to dispersive, pair-breeding clades [15,16].

Cockburn uses the distribution of Melanesian birds to illustrate his hypothesis. Mayr and Diamond [17] suggested that the taxa that failed to colonize islands in this region cannot fly long distances, whereas Cockburn suggests that breeding behaviour better explains the avifauna composition of Melanesia. He shows that cooperatively breeding taxa are conspicuously absent, whereas most pair-breeding clades have radiated throughout the area. However, this does not necessarily establish cooperative breeding as the cause of poor dispersal, and an alternative hypothesis is that inhibited dispersal and cooperative breeding are both consequences of low vagility.

Why are some species cooperative?

This new paper will influence our understanding of why species breed cooperatively. Cooperative species are more common and widespread than was recognized previously and ecological factors alone are unlikely to account for their distribution [6,7,18,19]. The review also highlights the regional imbalance among well studied taxa and that comparative analyses of ecological and life-history traits might be unreliable until biases are redressed [20]. For example, Cockburn argues that any apparent association between survivorship and cooperation is confounded by low survivorship at high latitudes. Similarly, his work emphasizes that ecological constraints hypotheses, which suggest that dispersal in cooperative species is inhibited owing to a shortage of mates or habitat [21], or is costly whilst young [22], must be treated as additional layers of explanation once the phylogenetic propensity for cooperation has been established. Knowledge of phylogenetic influences might also generate new predictions. For example, the ecological constraints hypothesis has been criticized for its lack of predictive power because all bird populations are constrained [21]. However it might now be possible to predict when juvenile birds facing ecological constraints will remain philopatric or form 'floating' populations.

Cockburn's review further erodes the notion that pair breeding is necessarily the ancestral state for passerine birds [10], and establishes cooperative breeding as a common trait with important macro-evolutionary consequences. However, such analyses, especially the ability to establish evolutionary causation, are hampered by the lack of data on many species. With further refinement of phylogenetic relationships among oscines, and an ever-expanding library of parental behaviour in birds, it is likely that the complex interaction of ecological and historical factors that favour the persistence or loss of cooperatively breeding will be described.

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