

Cooperative Breeding: A Question of Climate?

In some species, including humans, parents receive help with offspring care. A new comparative study suggests that birds breed cooperatively when environmental conditions vary. Further empirical and theoretical work will be required to understand the evolutionary significance of this insight.

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Why individuals should help with rearing the offspring of others, instead of investing fully in their own reproductive potential, is an evolutionary enigma with implications for understanding the bases of family and societal living [1]. Although cooperative breeding occurs throughout the animal kingdom, birds have been pivotal for testing its evolutionary origins. In fact, cooperatively breeding birds represent many of the most detailed long-term studies of individual species ever undertaken [2]. However, there has been little progress in extrapolating the insights revealed by these studies to predict the stark geographic differences in the distribution of cooperatively breeding species: depending on the location, zero to 30% of the local avifauna can exhibit cooperative behaviour. In a recent *Current Biology* paper, Jetz and Rubenstein [3] offer new hope; showing that cooperative breeding is more prevalent in regions that show high degrees of between-year variation in climate, particularly rainfall. This study sets a much-needed new benchmark in the level of detail as well as statistical rigor.

In vertebrates, cooperative breeding is chiefly viewed as a 'best-of-a-bad-job' strategy, undertaken when constraints prevent independent reproduction, forcing some individuals to pursue the alternative strategy of helping others [4,5]. However, previous attempts at identifying common constraints have failed: both extreme and benign climatic conditions have been proposed to account for cooperative breeding [3,4,6]. Nevertheless, until recently, progress in predicting which species should be expected to breed cooperatively has been hindered because our estimates of the distribution of cooperative breeding were based on flawed data,

which assumed that any species in which cooperative behaviour had not been recorded was non-cooperative [7]. In addition, assertions concerning the prevalence of cooperative behaviour were often based on qualitative impression rather than formal statistical analysis. For example, Trivers' suggestion "*Bird species with helpers ... are almost always tropical, subtropical, or Australian*" [8] can be rewritten without the phrase 'with helpers' without much loss of information [9]. Furthermore, assertions concerning the characteristics of the climate of one region versus another have sometimes been based on crude averages or qualitative impressions [10].

Jetz and Rubenstein [3] have attempted to remedy the difficulties mentioned above, combining a database estimating the parental care system of 9,310 species of birds (all but the seabirds) with fine-scale data on geographic range that could be mapped on to a 30 year climate record. In addition, they examine whether the variance as well as the mean levels of a given climatic variable (rainfall, temperature) are associated with the geographical (and hence ecological) distribution of cooperative breeding. Jetz and Rubenstein [3] report multiple associations, including an increase in the occurrence of cooperative breeding with increases in variance of temperature and rainfall as well as with increases in diet variability. The most convincing result, however, is that inter-annual variance in rainfall is positively associated with cooperative breeding in passerine birds (sometimes called 'songbirds'). This association is the most convincing one, as it stands strongest after information about the relatedness of the species being compared has been incorporated; thus, the effect is not a spurious association due to related species having similar ecologies and social systems because of common ancestry. This study is the most comprehensive

yet conducted, and the results offer new hope in understanding the evolution and dissolution of family-living in animals, including early humans.

Although Jetz and Rubenstein's study [3] represents a valuable first step, there are a number of empirical and theoretical caveats that will require additional attention before we can conclude that these insights represent a long-awaited breakthrough. First, the statistical power that emerges from such vast data sets can generate statistical significance with effect sizes of dubious biological importance. When the effect of variation in rainfall is tested without information about the relatedness of the species involved, the ability of the model to distinguish between cooperative and non-cooperative passerines is modest at best (about 12% of cooperative species are estimated to be so, while about 8% of non-cooperative species are also expected to be cooperative). When information of relatedness between species and higher taxonomic groups is included in the model, the prediction improves to about 22% versus 2%, respectively. This confirms earlier assertions that a considerable amount of variation is explained by ancestry, so there must be some additional unexplained feature in the evolutionary history of birds that needs to be taken into account [7]. However, even with this additional information about relatedness, the predictive capacity of variance in rainfall remains low [3,7,9].

The second difficulty of global correlations is that they can obscure recognition of independent processes affecting the trait of interest. For instance, most aspects of climate vary with latitude. In at least one bird family (Corvidae), cooperation has been repeatedly lost as birds have moved into more northerly latitudes [11], as expected from the extreme rarity of cooperative breeding in northern temperate environments. On the one hand, this supports the principal finding that inter-annual variation in climate is low at high latitudes [3]. On the other hand, the climate of northerly environments is distinguished by many closely correlated characters; it is therefore likely that many features of climate will be correlated with the type of social system. Just as for other conundrums, such as the latitudinal

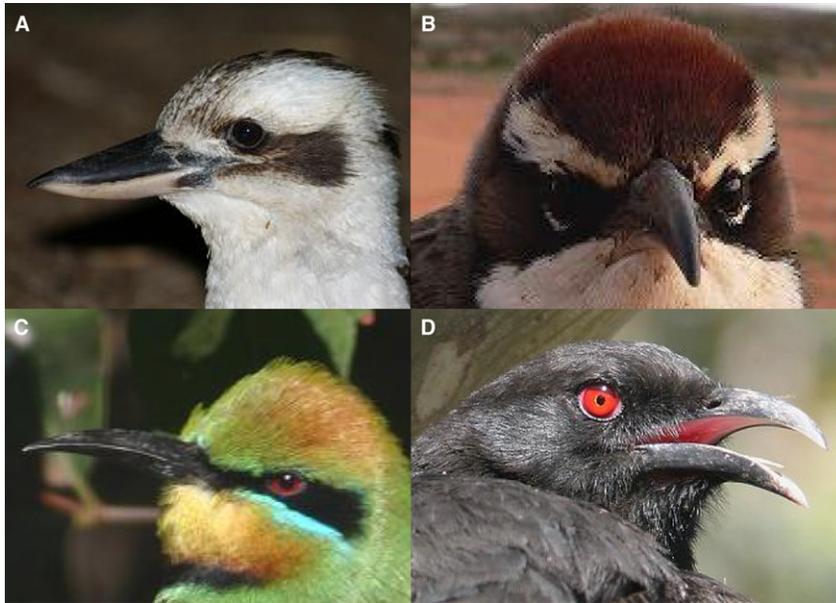


Figure 1. Breeding cooperatively.

Cooperative breeding is common in Australian avifauna where it can be associated with facultative helping in nuclear family groups with a single monogamous breeding pair (laughing kookaburra, *Dacelo novaeguineae* (A)), extended family units with plural breeding pairs (chestnut-crowned babbler, *Pomatostomus ruficeps* (B)) and colonies of migratory species (rainbow bee-eater, *Merops ornatus* (C)), as well as obligate helping in at least one that cannot breed successfully without help (white-winged chough, *Corcorax melanorhamphos* (D)). A current challenge is to understand the forces resulting in this diversity. (Photos: A.F. Russell (A–C) and Geoffrey Dabb (D).)

gradient in species diversity, identifying a correlation is a long way removed from identifying a cause, and statistical analyses conducted at the global scale are unlikely to unravel the primary cause of the gradient.

Third, Jetz and Rubenstein [3] divide their analyses between the passerine and non-passerine birds (loosely, songbirds and non-songbirds), which raises some problems. In a phylogenetic sense, passerines are nested deeply within the non-passerines, so the two groups do not represent a natural contrast. Indeed, elsewhere we [7] have argued that the starkest evidence of a phylogenetic effect on the distribution of cooperative breeding occurs within the passerines, which are treated as a homogenous group by Jetz and Rubenstein [3]. The Australian-derived oscine passerines are the most speciose group of birds — a vast radiation that has swept throughout the world once they ‘escaped’ from Australia. Although their non-Australian counterparts (the suboscines) occur throughout the old Gondwanan continents (South America, Africa, Australia and India), there are only enough suboscine species in the

Neotropics to allow meaningful comparisons. Large numbers of oscines and suboscines occur side-by-side in all habitats in the Neotropics, yet while the oscines are often highly cooperative (e.g. New World jays, mockingbirds, wrens, icterid blackbirds and tanagers), the suboscines are hardly ever so, despite the absence of any tractable life-history or ecological differences between the two groups [7].

A significant challenge has been not only to identify predictors of cooperative breeding worldwide, but also within the vast majority of clades of birds that are ‘... tropical, subtropical, or Australian’ [8]. The clades which are exclusively cooperative are typically species-poor [10], but there are sufficient families that allow drawing contrasts between cooperative and non-cooperative species. Currently, there appear to be few cases where cooperative breeding can be reliably predicted based on aspects of ecology, even where detailed phylogenies and trait sampling are available [11,12–14]. We suggest that further analyses will be needed in which the data are restricted to smaller geographical scales (i.e. tropics,

sub-tropics, Australia) and species from the same clade that vary in their degree of cooperation (Figure 1) [5]. This will permit direct tests of Jetz and Rubenstein’s [3] findings without the potentially confounding influences of including large climatic zones that lack cooperative breeders altogether, or species from vastly differing phylogenetic lineages which do not provide natural comparisons.

Jetz and Rubenstein [3] suggest that cooperative breeding might be favoured by selection when conditions vary from year-to-year, as helpers provide greatest benefits when conditions are poor. An alternative explanation is that helpers accumulate in variable environments as a consequence of population dynamics. Where conditions are variable and cooperative breeding arises through natal philopatry [4,5], favourable conditions will lead to recruitment of more offspring, hence creating additional potential breeders. When conditions deteriorate, those extra potential breeders may have few options but to become helpers. While an additional workforce might be beneficial to parents struggling to reproduce in poor conditions [15], there is also evidence that philopatry and helping can be enhanced by favourable conditions [4,16,17]. Future studies will need to dissect the chain of causation and determine whether or not cooperative breeding is selected for by environmental variability, or is an inevitable unselected consequence. Further, it is currently unclear whether relationships between inter-annual environmental variability and cooperative breeding arise because cooperation is favoured in some species when the environment is poor and others when it is favourable, or in all species because of both [6].

Finally, if cooperative breeding evolved because it facilitates fitness gains under poor ecological conditions, as suggested by Jetz and Rubenstein [3], we will need new theory to understand this. A valuable theoretical framework in this regard is bet-hedging, which models how individuals should maximise long-term fitness in variable environments [18]. In the context here, one possibility is that helping strategies evolve when conditions are unpredictable as a way of increasing the probability that individuals gain some fitness before

death. While selection on bet-hedging can shape any life-history character, the evolution of a helping strategy has not received explicit attention. In principle, mutations for helping as a bet-hedging strategy could evolve in offspring or in parent(s), with the latter arguably more likely because parent(s) and siblings would more likely all carry the 'bet-hedging mutation' than if it arises in a single offspring [19]. Future models of bet-hedging, cooperation and indirect genetic effects will provide an exciting new theoretical avenue for understanding the evolution of cooperative breeding.

Jetz and Rubenstein [3] offer new hope in the quest for a general selective pressure underlying cooperative breeding. We have outlined a number of directions we believe that future studies will benefit from pursuing. In addition, it is worth noting that other taxonomic groups offer independent tests. Mammals, although problematic because of their lower number of families, have the advantage that many families show both cooperative and non-cooperative species [5]. Finally, it is interesting to speculate whether increased environmental variability during the Pliocene, thought to have contributed to multiple adaptations in the hominin lineage [20], also selected for cooperative breeding.

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Cell Polarity: PIN It Down!

How do plants create and maintain cell polarity? Recent studies reveal a plant-specific mechanism, which links the static cellulose-based extracellular matrix to the dynamic localization of PIN auxin carrier proteins.

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Plants have evolved remarkable abilities to adjust growth and morphology in order to satisfy fluctuating environmental demands. They accomplish this by redefining the polarity both of entire tissues and of individual cells. The plant signaling molecule auxin is a key player involved in these adaptive aspects of plant development and contributes substantially to plant architecture. Developmental processes involving auxin require the activity of PIN-type

auxin carrier proteins, originally identified as landmarks for cell polarity in plants. Specifically, asymmetric polar distribution of PIN transport proteins in defined plasma membrane domains is a prerequisite for coordinating the transport of auxin in plant tissues [1].

Several studies on PIN protein localization have underlined the dynamic responsiveness of PIN proteins to a range of internal and environmental cues (Figure 1). Readjustments in PIN localization depend on mechanisms that facilitate their internalization from the plasma membrane by clathrin-dependent

endocytosis in conjunction with their subsequent recycling and transcytosis [2–4]. In addition to protein recycling, a fraction of PIN proteins appears to be subject to vacuolar targeting and subsequent degradation, allowing for further fine-tuning of auxin transport in response to environmental signals [5].

Regulatory determinants that actively modulate polar PIN localization involve reversible protein phosphorylation as well as variations in membrane sterol composition [6–10]. Nonetheless, identification of further molecular switches acting on PIN polarity is imperative, especially since plant cells have a complex extracellular matrix, the cell wall, which makes it even more difficult to envision a mechanism that enables neighboring cells to perceive external cues and convert them into a polar distribution of membrane proteins.