12 Cooperative Breeding in Birds: Toward a Richer Conceptual Framework

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In most organisms, care for offspring stops once the egg is provisioned, or else is dominated by just one parent. However, in some taxa, cooperation occurs between both the male and female parent, and parental care is shared. True cooperative breeding, where more than two individuals combine to rear a single brood of offspring, has also evolved many times, though its phylogenetic distribution is patchy, being particularly common in some groups of insects and in birds. By simple arithmetic, some of the individual carers in cooperative groups are assisting young that are not their own. As parental care is costly, this behavior is altruistic and requires special explanation within evolutionary theory, which predicts that behavior will be motivated by self-interest.

Cooperative breeding is troubling to theory precisely because of the stark simplicity of the situation. Consider eclectus parrots, where females are utterly dependent on male provisioning to feed themselves and their offspring. Females mate with many males each mating period and receive food for as much as ten months of the year as a consequence (Heinsohn et al., 2007). Yet females lay just two eggs, so most of the males cannot have sired the brood they provision.

Attempts to understand cooperative breeding have given rise to sophisticated theory (e.g., Gardner, West & Wild, 2011), increasingly clever experiments (e.g., Baglione et al., 2002), and some of the most intricate long-term studies of free-living organisms ever attempted, particularly among birds (Stacey & Koenig, 1990), where about 9 percent of species breed cooperatively (Cockburn, 2006). My purpose is not to review that literature, but to analyze how preconceptions and assumptions may have shaped the study of cooperative breeding. I will argue that the original questions that have guided the study of cooperative breeding in birds are declining sharply in heuristic value, and are increasingly hindering attention to a new set of questions, solutions to which will afford an opportunity for conceptual and theoretical synthesis, yet allow recognition of the incredible diversity of cooperative systems. In this review, I focus on the empirical literature on cooperative breeding in birds, though many of arguments recall debates that are well developed in the literature of social insects.

I also unashamedly concentrate in some detail on empirical examples from my own research group, as it is in these that I understand from bitter experience where conceptual straitjackets can be most misleading.

The Standard Framework: A Problem in Two Steps

The primary question of why some bird species breed cooperatively has traditionally been structured around two questions (Emlen, 1978; Brown, 1987). First, why in some species do young remain into adulthood on the territory on which they were born (natal philopatry) rather than dispersing to pursue independent reproduction? Second, given philopatry, why do they assist the adults on their natal territory to rear additional broods?

Philopatry

The problem of philopatry helps illuminate two problems that will recur throughout this discussion. The first difficulty is one of untested assumption. It makes sense to focus on philopatry as the critical phenomenon to be resolved only if cooperative breeding is inevitably (or at least largely) associated with individuals remaining with their parents on the natal territory, which leads to the formation of family groups (Emlen, 1995; Covas & Griesser, 2007; Ekman, 2006). Although it is certainly true that most *well-studied* species conform to this model, the issue of prevalence remains unresolved. Biased sampling can arise because species that live in family groups on year-round territories are unusually easy to study, for example by allowing easy detection of whether the size of the breeding group is greater than two. It also seems sensible to try and understand philopatry in taxa where it occurs, but assuming that philopatry and cooperative breeding are intimately intertwined can constrain the choice of study organisms and the questions addressed in analysis. Indeed, it is now clear that cooperative breeding occurs in many other circumstances, including family groups, completely unrelated individuals, and bizarre mixtures of the two (Cockburn, 1998). Without a great deal of additional work, it will be impossible to assign most cooperative breeders to these three categories.

It is also true that remaining philopatric to the natal territory is not a prerequisite for cooperative breeding, as we have seen in the case of eclectus parrots that move throughout the forest and feed females at more than one nest. For example, a recent compilation shows the prevalence of cooperative breeding is much higher than has previously been supposed (Cockburn, 2006). Many potential or actual cooperative breeders such as Asian babblers and neotropical tanagers do not live their lives on year-round territories, but spend a great part of their lives foraging in mobile multispecies feeding flocks (bird waves), only breaking away from the flocks to breed. None of these species have ever been the subject of detailed study, which is scarcely surprising

in view of the formidable difficulty of studying animals whose breeding site is unpredictable and whose nest may be hidden in the rainforest canopy.

However, an indication of the possibilities comes from weavers in the genus *Malimbus*. These birds were among the first tropical species whose nesting behavior was filmed, confirming the startling suspicion that whereas several birds cooperate to weave an impressive nest, only a single pair appeared to contribute to rearing the young (Brosset, 1978). Alexander Skutch (1987) went on to use this half-hearted assistance as the lowest possible level of cooperative behavior in his proposed hierarchy based on group selectionist philosophy, in which he asserted that helping other species was the pinnacle of the evolution of cooperation. However, recent study of the endangered *Malimbus ballmanni* has shown that the situation is even more curious than originally supposed. Although the supernumerary birds that do not initially provision the young follow the flock away from the nest that they have helped build, the mixed species flock may return many days later to the vicinity of the same nest. The supernumeraries then start provisioning, but only until the flock moves on, so they may help with rearing chicks for just a few hours in the entire nestling period (Gatter & Gardner, 1993). It remains unclear whether this help or the assistance with construction of the nest affects the fitness of the pair they assist.

The second difficulty is that while the evolution of natal philopatry is profoundly fascinating and a rewarding and insufficiently developed area of research, its relevance to understanding cooperative breeding may have been overestimated. As for many aspects of cooperative breeding (and studies of mating systems in general), investigation of philopatry in different cooperative species provides reasonably unequivocal support for all the competing hypotheses that have been proposed to explain its prevalence (e.g., Komdeur, 1992). In many cases this means that there is robust evidence that all these hypotheses are also untrue, in certain species in certain circumstances. Hence understanding philopatry is less critical than recognizing that it occurs.

To illustrate how confusion can arise, consider the hypothesis that philopatry arises and leads to cooperative breeding because opportunities to breed elsewhere are unavailable (the habitat saturation or ecological constraints hypothesis). There are two classical textbook examples of such constraints. First, in the Seychelles warbler, philopatry of daughters only arises once a certain population density is exceeded, implicating crowding in the occurrence of cooperative breeding (Komdeur, 1992). Second, in superb fairy-wrens, experimental removal of breeding pairs from territories fails to elicit any interest in the vacant territory from neighboring supernumerary males, but return of the female immediately prompts a neighbor to move in and pair with her, suggesting that the unavailability of unpaired females is the constraint on dispersal (Pruett-Jones & Lewis, 1990).

However, where one only one sex remains philopatric, as is true for both these species, the assumption of constraints can often produce logical inconsistency. In

Seychelles warblers, supernumerary males bud off small territories at the boundary of their natal territory to establish a vacancy (Komdeur & Edelaar, 2001a), raising the question of why females cannot use similar tactics. A likely explanation is that philopatric females often contribute eggs to the nest they help rear (Richardson, Burke & Komdeur, 2002), providing them with direct benefits that are more important than constraints in influencing the decision to remain at home. In superb fairy-wrens, the shortfall of females is itself largely a consequence of the obligate dispersal of young females (Cockburn et al., 2003), as most of these females die during dispersal as the result of the failure to obtain a vacancy (Cockburn et al., 2008b). We are therefore left with the dilemma that dispersal by one sex causes the shortfall in the other, which is hardly consistent with an insoluble constraint. The inconsistency is heightened by the red-winged fairy-wren, *Malurus elegans*, in which supernumerary females are also philopatric, and the incidence of cooperative breeding is much higher than in other *Malurus* species (Russell & Rowley, 2000), suggesting that in the genus the shortfall of one sex cannot be the primary influence shaping cooperation. Further clear evidence that prolonged philopatry can be beneficial rather than enforced through a constraint comes from species where there are limits to the numbers of brood-mates that are tolerated on the territory, and the philopatric individuals enjoy advantages over their dispersive brood-mates. In the best-studied example, direct lifetime advantages of philopatry have been convincingly shown in the Siberian jay (Ekman et al., 1999), and appear to be linked to the ability of the parents to procure safe access to food for their offspring (Ekman et al., 2000). Notably, this species does not breed cooperatively, though one of its congeners has been shown to do so (Jing, Sun & Fang, 2003).

Hence we are left with little insight other than the straightforward observation that in species with prolonged natal philopatry, there is the possibility that supernumerary family members will be available to help their parents raise offspring. However, there are also species with prolonged natal philopatry where help does not occur, and cooperative breeders where there is no natal philopatry; and we are poor at predicting why this is so.

Help

Numerous hypotheses have been suggested to explain why more than two individuals can care for offspring, but as I have reviewed this topic elsewhere (Cockburn, 1998), I will summarize these only briefly. Recent interest has surrounded five possibilities.

First, helping may provide future benefits, such as practice in rearing young, or production of a future workforce. Helping behavior may represent "rent" that allows courtship of future mates, inheritance of all or part of the territory, or a safe haven to wait for neighboring vacancies. Understanding how to assess these multigenerational advantages is in its infancy (Kingma, Hall & Peters, 2011), and this is an area that will unquestionably come under greater scrutiny.

Second, subordinates can gain direct access to at least some reproduction, subject to the important constraint that incestuous mating is rare or absent in most cooperative breeders (Cockburn, 2004; Koenig & Haydock, 2004). Where this constraint does not apply, it has long been known that in some species direct access to reproduction is shared in a reasonably egalitarian manner, though in species with low fecundity, reproduction needs to be summed over several broods to understand the extent of sharing (Haydock & Koenig, 2002; Millar et al., 1994). In other species, dominants gain most success, though in the majority of well-studied species, subordinates do gain significant access to reproduction unless constrained by incest avoidance (Cockburn, 2004). Why some species remain completely monogamous remains poorly understood. What is most bewildering about the contest between group members for reproduction is that it occurs within very many highly distinctive mating systems, and there is much less convergence between unrelated taxa than might have been anticipated. In an earlier review I showed that it was possible to recognize 22 distinct mating systems among the 30 species that had been subject to detailed molecular dissection of mating success (Cockburn, 2004), and that where different species had the same system, they were generally close relatives. Indeed, the sheer variety of cooperative systems, some of which will be illustrated below, represents a fundamental failure of our ability to understand the evolution and maintenance of cooperative breeding.

Third, there can be indirect (but immediate) access to fitness, by helping relatives to rear young. There is an obvious nexus between this hypothesis and the ability of philopatry to promote kin association. However, it is increasingly clear that kin association can arise from diverse mechanisms in addition to philopatry (Hatchwell, 2009, 2010). Kin selection has played a crucial role in the development of theory pertaining to cooperative breeding, and the eusociality found in other taxa (Hamilton, 1964a,b). This theory and its empirical basis have recently been strongly attacked (Nowak, Tarnita & Wilson, 2010), but such attacks appear to be based on a straw-man trivialization of theory, and a dramatic underestimation of the power of inclusive fitness theory to make predictions that can and have been tested successfully (Gardner, West & Wild, 2011).

Indeed, studies of bird species have yielded sophisticated contextual and experimental evidence for kin-selected helping behavior. Remarkably, the best support has been from societies quite different from the model where philopatric young assist their parents to rear offspring. The most compelling results are from research by Hatchwell and his colleagues on long-tailed tits, where breeders that have failed in their own independent attempts seek out a relative with an intact nest and help with that breeding effort (Hatchwell & Sharp, 2006). The active choice confirms the crucial role of kinship. Although it has been argued that such failed breeder systems represent a transitional state to the complex state where helpers never attempt independent reproduction (Ligon & Burt, 2004), I know of no case where that is strongly indicated.

By contrast, there are many cases where such a transition is unlikely, primarily in species that produce several broods each season, so the failure of their first nest does not remove options for future reproduction.

Good evidence for kin effects also occurs in migratory species (Lessells, Avery & Krebs, 1994), and birds that breed in colonies (Covas et al., 2006). In another remarkable study from carrion crow breeding groups comprised of both philopatric and immigrant supernumeraries, the best evidence comes from immigrants, which preferred to help young to which they were likely to be most closely related, suggesting that they had actively chosen groups comprising relatives (Baglione et al., 2003).

It is true that in these cases active choice increases the probability of unambiguous detection of kinship effects. Indeed, definitive tests are difficult where only philopatric young have the opportunity to help, as there is no context to evaluate helping in circumstances where relatedness is low. It is nonetheless important to realize that kin selection can still work without any kin discrimination, provided that relatedness on average is reasonably high and that the actions of the subordinates enhance the output of the relatives they are assisting. However, it can be difficult to demonstrate such enhancement, because experiments often perturb far more than the amount of provisioning (Dunn & Cockburn, 1996; Jamieson & Quinn, 1997), and correlative studies are plagued by numerous confounding variables, most notably the difficulty of demonstrating unambiguously that extra provisioners improve productivity (Cockburn et al., 2008c). In philopatric species, high group productivity in the presence of help could indicate that supernumeraries provide a benefit, but it could also suggest that productive territories or parents are more likely to acquire supernumeraries. Alternatively, an absence of a correlation between help and productivity could arise because helpers only assist when help is beneficial (Reyer & Westerterp, 1985). Some progress had been made in developing statistical methods to overcome these problems, but the data requirements are formidable, and the methods remain rarely applied (Cockburn et al., 2008c).

Finally, despite claims to the contrary, kinship is irrelevant or of uncertain importance in the contemporary social systems of other avian cooperative breeders, most obviously where unrelated individuals collaborate (e.g., greater anis, Riehl, 2011), but also in many cases of "family" groups, where helping is provided even where relatedness is unlikely, such as the fairy-wrens (Dunn, Cockburn & Mulder, 1995), or in an extreme case, helpers unrelated to the dominants are most likely to provision (white-browed scrubwrens, Magrath & Whittingham, 1997). These examples come from families where cooperative breeding is universal (Crotophagidae, Maluridae) or fairly common (Acanthizidae), suggesting that either kinship was unimportant in the evolution of complex social organization in some of the main clades where it now occurs, or perhaps more plausibly, that it has declined in importance as social evolution proceeded.

Summary

In summary, available evidence suggests that cooperative societies have diverse origins and evolve along idiosyncratic trajectories. Explaining this variation is unlikely to be achieved by focusing exclusively on what is an important but nonetheless specific case: natal philopatry leading to the formation of family groups on year-round territories. Even within these species, testing any of the links in the causal chain (constraint leads to philopatry leads to kin association leads to kin-selected cooperation) is technically challenging and rarely accomplished.

Can We Unpack the Diversity Using Comparative Analysis?

The usual approach to dissection of diversity is broad-scale comparative analysis. However, avian cooperative breeding has been quite resistant to such approaches. The difficulties can be illustrated by reviewing a number of recent analyses that have claimed to discern general patterns in the distribution or evolution of cooperative breeding.

First, in attempting to test particular hypotheses, it is possible to construct the analysis in ways that are biased toward supporting the conventional framework. Cornwallis and his colleagues (2010) recently analyzed what has become known as the monogamy hypothesis. According to this view, which originated in studies of cooperatively breeding insects, kinship between potential helpers and the broods they provision is higher when parents mate faithfully, as subordinates are likely to be helping rear their full sibs, whereas if the female mates promiscuously, the subordinates will often be caring just for half-sibs (Boomsma, 2007; Boomsma et al., 2011). Cooperation is therefore expected to arise more commonly in the case of true fidelity. Two of the results obtained by Cornwallis et al. (2010) provide support for this hypothesis. First, as predicted, evolutionary transitions to cooperative breeding are most likely when females mate monogamously, and loss of cooperative breeding is most likely when females are unfaithful to their mates. Second, in a more subtle result, they showed that there was little evidence for sophisticated kin discrimination when females are faithful, which is expected when a rule of thumb that presumes relatedness is reliable, not when fidelity was very low, when presumption of relatedness is unjustified. However, kin discrimination occurred at intermediate levels of fidelity. This study is fascinating, and will provoke further work, but in order to construct these contrasts it was necessary to define cooperative breeding as being confined to family groups. Hence, the construction of the question is heavily biased to support kin-based explanations of cooperation (Cockburn, 2010).

Second, there is the difficulty of how to treat the underlying variation in the trait. The simple and most commonly adopted approach is to treat cooperative breeding as a binary (yes/no) trait. For example, Jetz and Rubenstein (2011) recently used a global

analysis to argue that cooperative breeding is associated with interannual variation in rainfall, at least in the passerine birds that dominate avian diversity and include many transitions to and from cooperative breeding. In constructing this test all other parental care systems are lumped together as a single alternative state, so brood parasitism of the nests of other species and uniparental care by females or males are treated as equivalent to biparental care, which, as we have just seen, does not seem particularly sensible, as transition to group breeding from uniparental care is not expected because the pattern of relatedness in this case is less clear than when young are helping rear the young of their parents.

Third, particularly when sample sizes are extremely high, it is possible to obtain highly significant associations that provide negligible additional biological information. In the Jetz and Rubenstein (2011) study, the amount of extra variation explained over and above the well-known but poorly understood phylogenetic concentration of cooperative breeding is very slight (Cockburn & Russell, 2011).

Finally, choice of explanatory variables is itself problematic. Jetz and Rubenstein (2011) attempted a global analysis extrapolated from a more focused study on African starlings (Rubenstein & Lovette, 2007), which had implicated interannual variability as the best predictor of which species are cooperative. One of the difficulties in a global analysis is that most climatic and many other ecological variables will be strongly correlated with the best-known geographic predictor of cooperative breeding, a sharp decline in frequency at far northern latitudes (Cockburn, 2003; Ekman & Ericson, 2006). This not only makes interpretation of causation from correlation even more obscure than usual, but it fails to deal with the unexplained variation within the tropical and subtropical latitudes within which most birds live.

Finally, even if the correlation is the correct one, its interpretation would not be straightforward. Jetz and Rubenstein (2011) speculate that the benefits associated with help will be most pronounced in harsh conditions. However, although there is some empirical support for the contention that help is most likely and beneficial under harsh conditions (Covas, du Plessis & Doutrelant, 2008; Reyer & Westerterp, 1985), it has more often been shown that philopatry and helping are more likely under favorable conditions, perhaps because younger birds are more likely to have excess resources they can afford to donate to others (Baglione et al., 2006; Cullen, Heinsohn & Cockburn, 1996). Hence, the importance and theoretical implications of these observations remain uncertain.

These comments are not meant to indicate that comparative analysis will not help unpack the causes of cooperative breeding. However, progress may be greatest with a series of structured analyses that recognize the suite of different ways that prevalence of a trait can be influenced. For example, I have argued that cooperative taxa where at least one sex is highly philopatric may have different speciation dynamics than species that breed as pairs, because colonization of new habitats such as oceanic

islands, or via migration over hostile habitat, is unlikely unless both sexes disperse (Cockburn, 2003). This leads to macroevolutionary consequences, by restricting the diversity of cooperative clades, but also macroecological effects, as assemblages in recently colonized habitats will be dominated by pair-breeders.

A New Set of Questions

What can we do about this ongoing uncertainty and lack of progress? I believe we need to introduce new questions to focus research, and abandon the straitjacket that the traditional model has imposed. Progress will be furthered the most by acknowledging variation and trying to explain it. I believe that further investigation of five intimately related questions is likely to be extremely valuable.

First, why do the mating systems of cooperative breeders diverge so dramatically? Second, why does the role of kinship in cooperative breeding seem so obvious on the twigs of the evolutionary tree (e.g., among failed breeders and migrants), whereas the contemporary importance of kinship appears to be much less obvious in some of the clades where cooperative breeding is best developed? Third, how do societies proceed from facultative cooperative breeding to an inability to breed successfully as unassisted pairs? Fourth, why does cooperative breeding persist in social systems that are riven by conflict between the separate participants? Fifth, how do the underpinnings of cooperation in species that live in family groups compare to those in groups comprising unrelated individuals, and is transition from one state to the other possible?

Here I will argue that all of these questions can be answered within a common conceptual framework. In essence, once low levels of cooperative breeding arise, new evolutionary pressures arise for the participants. Solutions to these pressures will push lineages along idiosyncratic trajectories, and potentially obscure the conditions under which cooperation first developed. Under some circumstances, these trajectories trap the lineage on a peak in the adaptive landscape, meaning that the mating system is resistant to change, so that it persists despite changes in environment and speciation.

Obligate Cooperative Breeding: The Social Cradle

Some of the new evolutionary pressures are largely positive, offering benefits to all the participants. For example, prolonged kin association allows new types of investment by parents in their offspring. This in turn provides new opportunities for young. For example, learning may be facilitated as young are under less pressure to develop the skills they need to live independently.

The family Corcoracidae is an Australian passerine group with a long evolutionary history. Despite this, the family contains just two species, both of which occur over very large geographical ranges across long latitudinal gradients. Apostlebirds occur in

drier inland habitats, and white-winged choughs live in more mesic woodland habitats closer to the coast, though the range of both species overlaps extensively. Both species are primarily insectivorous, though apostlebirds have a more generalist diet, in particular with a greater dependence on seed. Despite ecological differentiation, the social organization and mating system of both species are nearly identical. They are obligate cooperative breeders, generally requiring at least four birds to rear young, as only a workforce of at least this size is capable of delivering sufficient food to the chicks (Heinsohn, 1992; Woxvold, 2004). Neither species is conventionally territorial, though the young are initially philopatric to the group in which they are born. Breeding success increases across all group sizes, creating the dynamic that small groups dwindle while large groups grow rapidly. However, conflict eventually develops within large groups, leading to formation of factions that attempt to disperse and breed.

These dynamics raise a series of problems. If the group dwindles, or drought or hostile conditions increase death rates among older birds, groups can be reduced to just juvenile birds that are incapable of breeding, or to a group incapable of successfully rearing chicks. In addition, when the size of large groups prompts dispersal, it is difficult for individuals or pairs of birds to disperse on their own, as independent reproduction would not be possible. Hence, the dispersing faction must exceed the critical group size, or the fragments must coalesce with other factions to exceed the critical group size. Genetic and behavioral studies suggest how these difficulties are resolved. In groups that have been stable for a long period of time, reproduction is dominated by just the dominant pair, but new groups that have been assembled from separate smaller groups share reproduction, though only one member of each faction ever gained success, and then only when they were supported by relatives (Woxvold & Mulder, 2008; Heinsohn et al., 2000). Garnering support therefore becomes critical, and it has been hypothesized that helping behavior itself becomes a signal of suitability as a faction partner. Young birds can scarcely afford to give up hard-won food. However, they ostentatiously carry food to the nest but then swallow it themselves, sometimes after lowering it into the bills of the nestlings. This suggests that they are signaling their suitability as a coalition member even when they cannot afford to lose food (Boland, Heinsohn & Cockburn, 1997).

The critical question is how does such extreme dependency on cooperative breeding arise in the first place? Arguments concerning the harshness of the local environment seem inadequate, given the extensive range of the birds and the stability of the system over millions of years, indicated by persistence through a speciation event after which considerable divergence in foraging habit occurred. At least in choughs, young do not learn adult foraging skills until they are four years of age (Heinsohn, Cockburn & Cunningham, 1988), and are fed for an extremely long period after fledging (Heinsohn, 1991). Prolonged learning affords many advantages, including a more nuanced exploitation of the resources in the local environment. However, it is easiest to sustain when a large workforce supports the young. This relaxed social cradle allows even slower

development to an extent that is extreme among passerine birds, but also ensures a workforce for parents attempting to rear young (Heinsohn, 1991). I suspect that this trajectory has stranded the birds on an evolutionary peak in which independent reproduction is no longer possible.

Winners Are Grinners: What Stabilizes Cooperation When Interests Differ?

In contrast to the favorable opportunities afforded by such a social cradle, it is also possible for costly antagonistic relationships to develop among the members of cooperative groups. There are three distinct disadvantages of group living, the first two of which are most pronounced among family groups. First, Hamilton (1964b) argued strongly that just as population viscosity can set the scene for kin cooperation, close association also leads to competition over resources and mating opportunities that limits the advantages of associating with kin (West, Pen & Griffin, 2002). The collapse of chough groups beyond a certain size illustrates these pressures. Second, a particular problem is posed by the limits to mating opportunities where incest avoidance prevails, or the cost of inbreeding if incest is not avoided. These difficulties and their idiosyncratic consequences have been reviewed by Koenig and Haydock (2004). Finally, although studies of cooperative breeders sometimes treat gender as irrelevant, there can be strong conflict of interest between males and females, and selection for one to exploit the other (Cockburn, 2004).

Cases of sexual conflict are rife. The extreme example where conflict leads to extraordinarily complicated relationships between group members (including kin) has been uncovered through my own work on superb fairy-wrens. These birds have played a central if ultimately completely misplaced role in the classic models of cooperation emerging from natal philopatry and kin selection (Brown, 1975; Grafen, 1984). Dominant males and females form a socially monogamous relationship to defend a year-round territory. All females disperse from their natal territory to breed, but males are more faithful to their natal territory than any other species thus far studied, with dispersal by and large confined to movements to immediately adjacent territories where all the males have died (Cockburn et al., 2008b, 2003). Many females fail to gain vacancies, so the sex ratio of breeding adults is strongly male biased, and as many as four subordinate adults can live with the dominant pair (Cockburn et al., 2008b). All males contribute to defense and provisioning of the young produced by the female on the natal territory (Dunn & Cockburn, 1996).

All males also become sexually active in their first and subsequent breeding seasons (Mulder & Cockburn, 1993). However, despite having access to as many as five sexually active males on her territory, the female always mates with a male from outside the group, whom she visits on a predawn foray three days before she lays the first egg (Cockburn et al., 2009; Double & Cockburn, 2000). Although she mates with her own partner (and subordinate males unless they are her sons) when she returns from the foray, the extra-group male is most likely to sire chicks, so most young are reared by

males other than their sire (Mulder et al., 1994). The female allocates a greater proportion of paternity to her mate when there are no helpers, probably because there is no alternative source of care (Mulder et al., 1994). Once she has helpers, nearly all paternity is allocated to the extra-group sires. What little paternity is made available is shared with helpers unrelated to the female, who, when present, gain about one quarter of all such success (Cockburn et al., 2008b,c).

Clearly this poses two disadvantages for the dominant males, which should undermine their willingness to breed cooperatively. Less paternity is available at home, and what is available sometimes has to be shared. However, helpers also pose an additional burden. Dominant males advertise to foraying females by singing in the dawn chorus (Dalziell & Cockburn, 2008). Helpers of attractive dominants join the chorus, and sing as close to the dominant as they are able, even though they are subject to attacks by him every single morning of the breeding season (Cockburn et al., 2009). Females arriving to mate with the dominant male are often confused by this parasitism, and helpers of attractive dominants are actually more successful at gaining extra-group parentage than average or low -quality dominants (Double & Cockburn, 2003). Helpers therefore undermine both the extra-group and within-group paths to reproductive success available to dominant males. Remarkably, there do not appear to be any compensating advantages. Helpers do not increase the productivity of the territory, which might have increased their chance of siring at least some offspring within the brood (Cockburn et al., 2008c). Males with helpers are able to feed less (Dunn & Cockburn, 1996), and do convert some of that advantage into more time courting neighboring females (Green et al., 1995), which they do by a dramatic dance display. However, there is strong evidence that female preference is finalized before the breeding season starts, so such additional display is unlikely to enhance male attractiveness (Green et al., 2000). Nor are there future benefits, as males with helpers are not more likely to survive until the following breeding season (Cockburn et al., 2008c).

By contrast, the breeding female gains considerable advantages from breeding cooperatively. Not only is the need to allocate the dominant some paternity removed (Mulder et al., 1994), but female survival to breed again is greatly enhanced (Cockburn et al., 2008c). This is initially surprising because while females with helpers reduce feeding rates, they do so to a lesser extent than males, so would be expected to achieve less benefit. This paradox has been resolved by the discovery that females achieve the survival advantage by laying smaller eggs (Russell et al., 2007). Their young are not disadvantaged, because the reduced investment in eggs is fully compensated by higher provisioning rates at nests where more than two individuals provision. Hence, females completely monopolize the advantages of cooperative breeding.

Initially such monopolization seems completely unstable, yet all but one of the comparatively old and species-rich genus *Malurus* share a mating system based on the curious combination of extra-group mating and cooperative breeding, despite being

found in almost every habitat in Australia and New Guinea. The mating system is thus extremely resistant to evolutionary change.

The strongest direct evidence that these tensions eat at the heart of fairy-wren society come from experiments that trigger behavior never seen in unmanipulated populations. In the first, helpers were removed for the week leading up to egg-laying (Dunn & Cockburn, 1996). This manipulation was expected to increase confidence of paternity for the dominant males, and hence induce increased provisioning. Instead, females refused to proceed with the nesting attempt, either resorbing the eggs, abandoning them once they were laid, or divorcing the male and moving elsewhere (Dunn & Cockburn, 1996). In the second experiment, helpers were removed for 24 hours at different times of the year and then returned to the group. It was expected that removal during the nestling phase would prevent load-lightening by the adults, and force them to feed at the rate of unassisted dominants. Dominant males by and large ignored the removal outside the provisioning period, but did react when there were nestlings to be fed. However, they did not change their provisioning rate at all, but attacked the helper repeatedly on his return, and chased and harassed him for the next couple of days (Mulder & Langmore, 1993). The response was so severe that the experiment was terminated for ethical reasons. How can these results be interpreted? It seems that the dominant pair have clear expectations of the resources they can obtain from other group members. Females expect a level of provisioning from dominant and subordinate males, and dominants expect provisioning from subordinates.

Disentangling the path to evolution a system of this intricacy will always involve speculation, but I believe the following is the most plausible sequence, driven by the ploy and counterploy that arises from the conflict between males and females.

1. Females face fierce competition for vacancies and are selected to settle with a minimum of prior assessment (Cockburn et al., 2003).
2. They compensate for lack of mate choice by seeking extra-pair fertilizations (Møller, 1992).
3. Males increase courtship of extra-group females in response and are able to do this by coercing care from subordinates (Mulder & Langmore, 1993), which allows the dominants to lower their own provisioning rate (Dunn & Cockburn, 1996).
4. Females take advantage of the coercion to increase the cuckoldry rate to a level that males would not usually tolerate (Mulder et al., 1994), and, by imposing progressively stronger sexual selection on males (Dunn & Cockburn, 1999), tip the balance in male fitness toward extra-group mating success.
5. The chief target of selection changes from the brilliance of plumage and courtship to the amount of time males spend displaying, so only the small number of males that can display continuously for months before the breeding season are attractive (Cockburn et al., 2008a; Dunn & Cockburn, 1999).

6. Females need to be able to find these males when they become fertile and seek them on their territories while they are advertising at dawn (Double & Cockburn, 2000). This locks males into needing a territory in order to be successful.
7. Females appease their own mates by copulating with them on their return (Cockburn, unpublished data).
8. Sperm competition arises between the extra-group and home male, leading to production of massive ejaculates that take time to replenish (Mulder & Cockburn, 1993; Tuttle & Pruett-Jones, 2004, 2007).
9. Females mate earlier and earlier to avoid sperm depletion of the attractive extra-group males (Double & Cockburn, 2000).
10. Subordinates (and unattractive dominants) exploit the uncertainty faced by females seeking attractive males in the dark by displaying parasitically in close proximity to him (the hidden lek hypothesis), increasing their own benefits of participating in the system (Cockburn et al., 2009).

This system achieves resilience to the collapse that would ensue if dominant males refused to provision chicks, because of the implications of high variance in reproductive success. Although in fairy-wrens this heterogeneity is affected to an unusual extent among cooperative breeders by sexual selection, virtually all studies of avian cooperative breeders report high variance among individuals that leads to proliferation of particular lineages (Stacey & Koenig, 1990). Regardless of the source, the variation generates real winners and, as a corollary, and much more commonly, losers. In fairy-wrens, most males are unattractive and perform poorly, so virtually all the reproductive success they obtain comes from mating with their own partner, as it is only subordinates of attractive dominants that are likely to achieve substantial fitness gains via the parasitic route. Although within-group mating is reduced in the presence of subordinates, the dominant male is always oldest, and it is feasible that the subordinates are his only sons. Low-quality birds are thus obliged to make the best of a bad job and cooperate with the female in rearing young, allowing her to monopolize the benefits of the cooperative system.

However, it is the extreme success of the winners that drives the evolution of the society, as most offspring will be progeny of these high-quality birds. For these birds, the convoluted evolution of the society constrains their behavior in a variety of ways. First, attractive dominants require a territory on which they can be found, and can gain reproductive benefits there, even though within-pair fertilizations are only a small component of their success. Therefore, they might as well have their cake and eat it too.

This line of argument has been challenged by the discovery that purple-crowned fairy-wrens, while remaining cooperative breeders, have secondarily reverted from a society based on extra-group mating to become genetically as well as socially monogamous (Kingma et al., 2009). The only clear distinction between this species and

its congeners is the configuration of its habitat, which is linear rather than spread across the landscape. The linearity arises because the species specializes on the riparian habitat that occurs along rivers and streams in northern Australia, many of which are filled with water only seasonally. Birds have no neighbors along most of the length of their territories, encountering other birds only at the ends of their territories. Kingma et al. (2009) speculate that genetic benefits from extra-group mating are unlikely to be available, as the probability that a female will have a high-quality male increases linearly instead of exponentially with the number of territories traversed, in contrast to the case of species living in a more complex landscape. The difficulty with this hypothesis is that most extra-group mating in well-studied species of fairy-wrens is over just a short distance, where this effect of the difference between the two landscape configurations would remain modest (Double & Cockburn, 2000, 2003).

An alternative hypothesis is that the system collapses because signaling by high-quality males is compromised in linear habitats, undermining the benefits to both males and females. Males advertising from beyond immediately neighboring territories can only be accessed if females fly past the display sites of males on intervening territories, sharply increasing the risk of parasitism to the males, and diminishing the likely returns to the female. The system is thus jeopardized for both parties in the mating transaction and is undermined by a condition at the top of the hierarchy of male-female conflict (selection for parasitism) rather than a lower-level condition that has been obscured by subsequent coevolution.

This model has been worked through in such length in part to illustrate the extraordinary complexity of some cooperative systems, but also to demonstrate how the endpoints of evolution can be fundamentally distinct from the founding conditions.

Can Mating Systems Transition from Families to Unrelated Groups?

What of cooperative breeding among unrelated individuals? It seems likely that conflict of interest between males and females over mating opportunities may once again be the explanation for most of these cases. In the best-studied species, the dunnock, the female incites supernumerary males to mate with her in order to persuade them to feed at her nest, which in turn increases her productivity (Davies, 1992). Males are sensitive to the risk of cuckoldry and apportion their care according to the proportion of time they have monopolized access to the female (Davies, 1992).

It has been suggested that such conflicts impose an upper limit on the number of males that could be induced to participate (Hartley & Davies, 1994). Unfortunately, the theory pertaining to this issue remains in its infancy (Johnstone, 2011), but there is empirical evidence that sometimes large coalitions of males may participate. In two of these cases (brown skuas and Galapagos hawks), there has been remarkable convergence on a system where multiple males spend a long apprenticeship in bachelor flocks on land unsuitable for breeding, and form coalitions to overthrow the males

breeding on prime territories elsewhere. On gaining a territory, these birds copulate with the female in an egalitarian fashion, and reproductive dominance is only gained when the other coalition members die. However, this also exposes the long-lived victor to a risk of overthrow by a new coalition of younger birds (Faaborg et al., 1995; Millar et al., 1994). By contrast, in eclectus parrots, large numbers of males can attend an individual female, but they do so facultatively rather than by becoming a member of a permanent group (Heinsohn & Legge, 2003; Heinsohn, 2008). Two subtleties explain this unusual system. First, males can actually attend several nests. Second, there is extreme heterogeneity in female reproductive success, driven largely by failure of nesting attempts due to flooding and predation, prompting males to direct care to high-quality females and their nests (Heinsohn & Legge, 2003; Heinsohn, Legge & Endler, 2005). Perhaps the most curious feature of this system is that in this case the females have evolved to become utterly dependent on the males. In order to defend quality nest sites, they occupy the nest cavity for as much as ten months of the year and are dependent on males for their own food throughout that time.

A mitigating circumstance that unites these three species is that the males in each case are potentially very long-lived (Faaborg & Bednarz, 1990; Millar et al., 1994; Heinsohn & Legge, 2003). Thus, despite the low clutch size in each species, males are likely to gain access to parentage over time, and molecular studies reveal that success by a male in one brood does not predict his success in later broods, so when integrated over many years, all males may gain direct reproduction from attending females (Faaborg et al., 1995; Millar et al., 1994; Heinsohn et al., 2007). We can therefore predict that large cooperatively polyandrous groups are likely to be found only in long-lived species.

Occasionally, cooperative breeding among unrelated individuals becomes obligatory. Riehl (2011) has shown that greater ani pairs cooperate to lay in and provision and defend a joint nest, despite considerable tensions involving initially tossing the eggs from other pairs from the nest. Despite these costs, reproductive success increases as the number of pairs contributing increases because of enhanced defense against nest predators. Once again, success at one nest does not predict success at subsequent nests, suggesting that reproduction is shared over time.

However, the transition to this state is even more difficult to explain than other obligate cooperative societies. One possibility I believe requires further investigation is the possibility that kin association could provide a founding condition for social evolution but be completely obscured by subsequent evolution. I know of no particularly convincing demonstration that this is the case, but there are numerous cases where the signature of kinship appears to have been diminished by a progressively greater role for unrelated helpers. For example, in *Manorina* miners, as in eclectus parrots, males within colonies can help at many nests, and nests are provisioned by very large numbers of individuals. While there is an underlying signature of kinship

that predicts provisioning rate, a great deal of the assistance is from unrelated individuals (McDonald, Kazem & Wright, 2009; Wright et al., 2010), which possibly gain benefits from subsequent mate acquisition. The transition from a condition where kinship is all important to one where mate acquisition becomes most important and a role for kinship disappears is certainly feasible.

Conclusions

In summary, I contend that discussions of cooperative breeding in birds have overemphasized ecological constraints and philopatry, forcing a restricted view of the extraordinary diversity of cooperative systems within birds. An alternative view focuses on the diversity and extraordinary evolutionary trajectories of cooperative lineages and recognizes that the evolutionary consequences of cooperative breeding may often obscure the founding conditions under which cooperation evolved. For example, kin selection may be a crucial founding condition but may diminish in importance within lineages. These evolutionary consequences of cooperation can be both mutualistic, allowing obligate cooperative breeding to evolve, and antagonistic, forcing complex mating arrangements. Both forces can strand lineages on an adaptive peak from which movement is difficult, stabilizing complex systems over evolutionary time. Attention to these possibilities will allow both theoretical and empirical progress.

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This book was set in Stone Sans and Stone Serif by Toppan Best-set Premedia Limited, Hong Kong. Printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

Cooperation and its evolution / edited by Kim Sterelny, Richard Joyce, Brett Calcott, and Ben Fraser.
p. cm.—(Life and mind: philosophical issues in biology and psychology)
"A Bradford Book."
Includes bibliographical references and index.
ISBN 978-0-262-01853-1 (hardcover : alk. paper)
1. Evolution (Biology)—Philosophy. 2. Evolutionary psychology. 3. Cooperation. I. Sterelny, Kim. II. Joyce, Richard, 1966–. III. Calcott, Brett. IV. Fraser, Ben.
QH366.2.C657 2013
576.8–dc23
2012025348

10 9 8 7 6 5 4 3 2 1

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