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Edited by Walter D. Koenig, Janis L. Dickinson

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Chapter

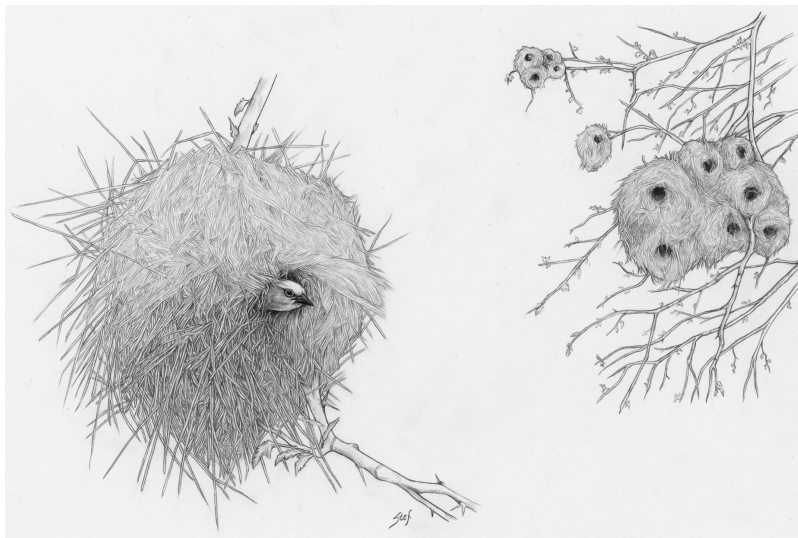
20 - Synthesis: Cooperative breeding in the twenty-first century pp. 3
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Synthesis: Cooperative breeding in the twenty-first century

Walter D. Koenig, Janis L. Dickinson, and Stephen T. Emlen



Introduction

One result of putting together this book was the realization that the field is less unified than it was 25 years ago when the prior book summarizing studies of cooperative breeding was published (Stacey and Koenig 1990). The focus at that time was largely on territoriality and ecological constraints as drivers of cooperative breeding in birds. Since then, the field has diversified both empirically and theoretically, encompassing an ever-widening range of social organizations from a broader suite of

habitats and geographic locations. We were surprised to discover how enlightening, yet difficult, it was to try to integrate this amalgam of long-term studies into a coherent framework. We admit that this was somewhat disappointing for us, who, as senior workers in the field, had hoped to generate a “grand synthesis.” It bodes well, however, for students interested in pursuing studies of cooperative breeding, because it indicates significant potential for further discovery and innovation.

As the grand synthesis remains elusive, we have instead elected to summarize a subset of issues

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drawing from the chapters in this book, moving beyond a summary in two ways. First, we emphasize the importance of distinguishing different kinds of group members based on their reproductive options; this is critical for generating the correct comparisons needed to understand which factors drive the evolution of cooperative breeding. Second, we analyze hypotheses that have been proposed for the ecological factors important to the evolution of delayed (or local) dispersal and helping behavior, two of the key features of cooperative breeding. Our goal is to provide a framework in these key areas that will facilitate future advances.

Forms of cooperative breeding and key factors in its evolution

Group structure and ecology

As already pointed out, cooperative breeding is not a unified phenomenon. At one end of complexity are nonbreeding helpers that are offspring of the breeders and have delayed, or at least localized, dispersal, while at the other are species exhibiting cooperative polygamy and various forms of plural breeding. Not infrequently, nonbreeding helpers co-occur with cooperative polygamy and plural breeding with variation in whether there is delayed dispersal, localized dispersal, or even coloniality.

Cooperative polygamy and plural breeding are particularly variable phenomena (Brown 1987), and we still do not have a good handle on all their various forms, because only a fraction of species known to exhibit such behavior have been studied in detail and because no doubt many have yet to be discovered. This book thus represents the range of cooperative breeding systems that are currently being studied intensively, not the diversity of all such systems. Preliminary studies of species such as the greater vasa parrot (*Caracopsis vasa*) of Madagascar, in which females copulate with and are fed by multiple unrelated and nonterritorial males (Ekstrom et al. 2007), the moustached warbler (*Acrocephalus melanopogon*), in which unrelated floater males assist in incubation, feeding of nestlings,

and defense of chicks (Fessl et al. 1996), and several of the other species mentioned by Cockburn (2004) suggest that many variants of cooperatively breeding remain to be investigated.

In the earlier volume of long-term studies, Smith (1990) pointed out that most cooperative breeders live on relatively stable, all-purpose territories, and this remains true for the majority of species discussed here, at least during the breeding season. Notable exceptions, however, include the long-tailed tit (*Aegithalos caudatus*; Chapter 3), which is non-territorial even when breeding; chestnut-crowned babbler (*Pomatostomus ruficeps*; Chapter 9), which have large, overlapping home ranges; and the grey-capped social weaver (*Pseudonigrita arnudi*), which is also nonterritorial and lives in relatively stable colonies (S. T. Emlen, unpubl. data; see illustration at beginning of chapter). Group sizes of many cooperative breeders are relatively small (<10; Smith 1990), but the spatiotemporal distribution of resources favors larger aggregations in others. Such species include the superb starling (*Lamprolornis superbus*; Chapter 11), in which groups can contain up to at least 40 birds, and some of the species discussed in the later chapters of this book, in which group sizes range from several dozen (in the fish *Neolamprologus pulcher*; Chapter 16) to upward of 75–80 individuals in banded mongoose (*Mungos mungo*; Chapter 18) and several hundred individuals in naked mole-rats (*Heterocephalus glaber*; Chapter 19). Cooperative breeding in vertebrates is clearly not just restricted to small groups of territorial species.

Extra-group parentage and its relationship to kinship

In the past 25 years significant advances to our understanding of cooperative breeding have come from molecular parentage analysis. In some cases it has turned out that the genetic mating system parallels the social mating system, and thus the molecular era has made little difference in terms of understanding social behavior. In red-cockaded woodpeckers (*Picoides borealis*; Chapter 4) and Florida scrub-jays (*Aphelocoma coerulescens*; Chapter 5), breeding pairs are socially and genetically monogamous, whereas extra-pair paternity

occurs, but is relatively uncommon, in long-tailed tits (Chapter 3). In other species, however, data on extra-pair paternity have led to significant reinterpretation of the breeding system.

Two of the more notable species where parentage analysis has altered our understanding of the social system are the Seychelles warbler (*Acrocephalus sechellensis*; Chapter 12) and the superb fairy-wren (*Malurus cyaneus*; Chapter 8). In Seychelles warblers, 44% of subordinate females lay eggs, although they were originally thought to be nonbreeding helpers, and a similar proportion of offspring are fathered by males from outside the group, thus altering earlier conclusions about the fitness benefits of helping in this species. In the superb fairy-wren, the incidence of extra-pair parentage is such that the genetic and social mating systems bear almost no relationship to each other. With extra-pair parentage on the order of 61% of offspring, among the highest found in any wild population, monogamy is clearly not required for the maintenance of cooperative breeding, despite evidence, supported by comparative phylogenetic analyses, that monogamy is associated with the evolutionary transition to complex societies in both birds and mammals (Cornwallis et al. 2010; Lukas and Clutton-Brock 2012).

The rationale for the hypothesis that monogamy is fundamental for the evolutionary transition to cooperative breeding is based on the assumption that genetic monogamy enhances relatedness between helpers and the offspring they help raise (Boomsma 2009). While this is true in some social insects, in which breeder turnover can be low enough that relatedness is unlikely to change significantly during the lifetime of a helper, it does not apply to vertebrates, whose relatedness to potential recipients of help frequently changes, most commonly when a parent dies and is replaced, thereby cutting relatedness of a helper to subsequent nestlings in half (Emlen 1995, 1997).

A second problem with this assumption is that it fails to consider the effect of extra-pair paternity on outside options. In such situations, what matters, in addition to the costs and benefits of helping, is relatedness of helpers to the young they would help raise, compared to their relatedness to the young they would parent were they to breed independently. In particular, a son's

relatedness to half-sibs resulting from extra-pair paternity is $r = 0.25$, whereas his relatedness to extra-pair young in his own nest is $r = 0$ (Dickinson et al. 1996). Thus, counterintuitively, extra-pair paternity can lead to the situation in which sons in cooperatively breeding vertebrates are *more* closely related to young in their parents' nest than they would be to young in their own nest (Dickinson et al. 1996; Kramer and Russell 2014). Indeed, if success at extra-pair paternity increases with age, as postulated by the delayed extra-pair benefits hypothesis described in Chapter 2, female promiscuity can actually *increase*, rather than decrease, the future direct and the future indirect benefits of helping for young males. This can be true even if helpers are unable to discriminate extra-pair from within-pair young and instead base their decision to help on their presumed relationship to the breeders, as is typically the case for cooperatively breeding vertebrates (Kramer and Russell 2014).

Inbreeding avoidance and reproductive skew

When cooperative breeding groups are extended families, a primary factor that restricts breeding on the part of helpers is incest avoidance (Koenig and Haydock 2004). The value of using incest avoidance to make a priori assumptions about the breeding status of different kinds of "helpers" is discussed in greater detail in the next section.

In most cases, incest is reduced through immigration, which provides unrelated individuals that can be chosen over kin as mates. Three species discussed here provide intriguing counterexamples, however. First are, once again, superb fairy-wrens (Chapter 8), in which social pairs are often first-order relatives; nonetheless, the high incidence of extra-pair fertilizations avoids any significant cost to such incestuous social pairings. Second is the banded mongoose (Chapter 18), in which groups are founded by unrelated individuals, but the permanent retention of philopatric offspring of both sexes leads to increased relatedness between breeders within groups over time, resulting in an extraordinarily high incidence of brother-sister and father-daughter incest. Last but not least is the naked mole-rat

(Chapter 19), where the mating system appears to be one of facultative incest.

The evolutionary implications of incest in these two latter species are, however, unclear. In the mongoose, the strikingly high levels of incest do not appear to lead to increasing levels of homozygosity among offspring, perhaps because of lower survivorship (inbreeding depression) among inbred offspring. Meanwhile, eusociality in Damaraland mole-rats (*Fukomys damarensis*), for which there is no indication of high levels of incest (Chapter 19), counters the hypothesis that inbreeding has played a key role in the evolution of eusociality in this taxon (Reeve et al. 1990). Indeed, whether inbreeding leads to increased relatedness and thus plays an important role in driving social behavior in any vertebrate remains an open question, whereas incest avoidance is clearly important in nearly all systems in which adult relatives find themselves in a position to potentially mate with each other.

Eliminating individuals constrained by incest avoidance leads to more insightful examination of reproductive competition (skew) within groups (Emlen 1996), which remains an important issue relying heavily on genetic analyses. Reproductive skew is examined in several of the species in this book that exhibit some form of cooperative polygamy. As with other aspects of cooperative breeding, skew is highly variable, with reproduction being largely or entirely monopolized by a dominant pair in western bluebirds (*Sialia mexicana*; Chapter 2) southern pied babblers (*Turdoides bicolor*; Chapter 7) and meerkats (*Suricata suricatta*; Chapter 17), less strongly monopolized by a dominant pair in chestnut-crowned babblers (Chapter 9) and banded mongooses (Chapter 18), and shared equally among joint-nesting females and cobreeding males in acorn woodpeckers (*Melanerpes formicivorus*; Chapter 13), at least when taking into consideration “switching” of paternity across nesting attempts. Currently we still have relatively little understanding of the factors driving these differences, although it is by means of such studies that our empirical knowledge of reproductive skew may eventually catch up with the plethora of theoretical models addressing this issue (Magrath et al. 2004; Shen and Reeve 2010; Nonacs and Hager 2011).

What is a helper?

Distinguishing different kinds of helpers

The above example highlights a key issue concerning not only family dynamics, but the very definition of helpers (often referred to as “subordinates” or “auxiliaries”). In particular, there are several categories of “helpers” in cooperative breeding systems that are frequently not clearly distinguished, despite the fact that the potential and means of gaining fitness within groups have long been known to be very different.

As a relatively simple example, consider white-browed scrubwrens (*Sericornis frontalis*). Whittingham et al. (1997) and Magrath and Whittingham (1997) described the behavior and differing degrees of paternity achieved by subordinate “helper” males in three contrasting circumstances. The first (Figure 20.1a) is a subordinate male that is the offspring of the dominant female. Such individuals, which may or may not also be the offspring of the dominant male, feed young at the nest but never achieve any paternity. The second (Figure 20.1b) is a subordinate male that is unrelated to the dominant female because its mother has died and been replaced by a stepmother. Subordinates in this situation achieve paternity *in some nests*; that is, they share reproduction with the dominant male, but unequally, and contribute to nestling care even when they have no paternity in the nest. The third (Figure 20.1c) is a subordinate male that is unrelated to both dominants, most commonly (but not necessarily) because he is an immigrant. Subordinates in this position share paternity more or less equally with the dominant male and, once again, provision offspring (i.e., help). Note that in all three cases we assume no extra-group paternity and thus the social parents are also the genetic parents; we will return to the case of extra-group parentage later.

Although there are multiple ways that the subordinates in Figure 20.1 can be categorized, a criterion that is key to interpreting helping behavior is whether the subordinate male helper is or is not the offspring of the dominant female, since this determines whether he potentially shares paternity, as in Figures 20.1b and 20.1c, or not, as in Figure 20.1a. In other words,

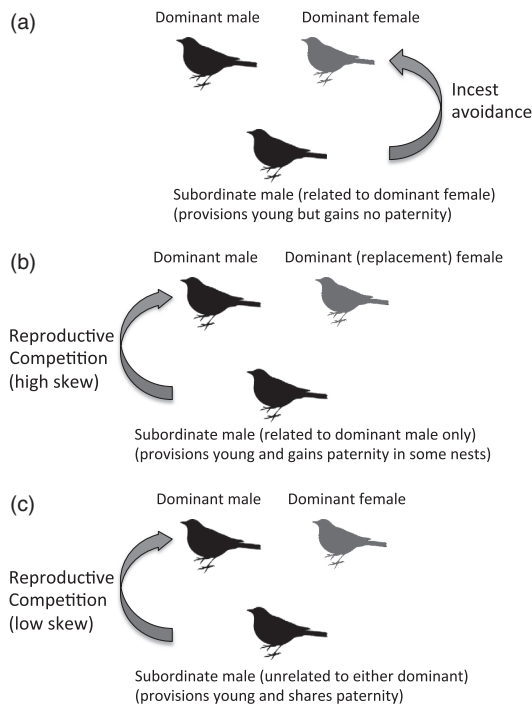


Figure 20.1. Different kinds of “helpers” illustrated by the three social situations in which subordinate male white-browed scrub-wrens find themselves. (a) A subordinate male living with a breeding pair, the female of which is the subordinate’s mother. The subordinate is constrained from breeding by incest avoidance with the dominant female; he provisions young but never gains paternity within the group. (b) A subordinate male living with a breeding pair, the male of which is the subordinate’s father and the female of which is a replacement (stepmother). The subordinate’s successful reproduction is limited by reproductive competition with the dominant male; the subordinate provisions young and gains paternity in some nests. (c) A subordinate male living with a pair, neither of which is related to the subordinate. As in (b), the subordinate provisions young and competes for paternity with the dominant male. However, he is more successful (skew is lower), and the subordinate shares paternity relatively equally with the dominant male.

the classification scheme most relevant to biological insight determines status based on whether the subordinate is a nonbreeding helper due to incest avoidance with the opposite-sex dominant (Figure 20.1a) or

reproductive competition with the same-sex dominant (Figures 20.1b and 20.1c).

This distinction defines two kinds of subordinates in a way that has been around at least since Reyer’s (1980, 1990) work on pied kingfishers (*Ceryle rudis*) describing “primary” helpers that are offspring helping to raise younger siblings (subordinates that do not breed because of incest avoidance) and “secondary” helpers that are unrelated immigrants whose helping behavior is part of a strategy by which they may eventually replace the dominant male and mate with the breeder female (subordinates that do not breed due to reproductive competition). Failure to recognize the difference between the two types means failing to acknowledge two very different and critically important evolutionary factors driving their helping behavior: primary helpers gain indirect fitness benefits while secondary helpers help in order to gain the future direct fitness benefits of breeding if and when they succeed in replacing the dominant male.

Although we use white-browed scrubwrens and pied kingfishers as our examples, the distinction between different types of subordinates is quite general and applicable to almost any cooperative breeding system, regardless of its complexity. It is therefore important to emphasize what does and does not distinguish the two kinds of subordinates.

First, the evolutionarily interesting distinction between the two types of subordinate helpers is *not* whether they are or are not successful at reproduction. Note that the subordinate in Figure 20.1b only sires offspring in *some* broods, and thus his status could easily be misconstrued if determination was based on genetic information alone. Conclusions based solely on parentage analyses are potentially misleading, even in the absence of extra-group paternity (see also Chapter 7).

A problem arises, however, when reproductive skew is strong and subordinates, despite being unrelated to the opposite-sex breeder at a nest, never (or at least very rarely) parent offspring, as is the case for secondary helpers in pied kingfishers and subordinates in species such as western bluebirds (Chapter 2), long-tailed tits (Chapter 3), pied babblers (Chapter 7), and meerkats (Chapter 17). Such nonbreeding individuals can reasonably be (and often are) referred to as

nonbreeding helpers, but are nonetheless distinct from helpers whose reproduction is limited by incest avoidance rather than reproductive competition.

Second, the distinction between the different kinds of subordinate helpers is only partly determined by whether they are helping to raise related offspring or not. In general, subordinate male helpers that are offspring of the breeding female (Figure 20.1a) are helping to raise what are at least half-siblings. Subordinate male helpers that are unrelated to the breeding female may or may not be helping related nestlings, depending on whether they are (Figure 20.1b) or are not (Figure 20.1c) related to the dominant male. Making these distinctions leads to interesting predictions about how much effort these different kinds of helpers should devote to cooperative behaviors and whether they should stay in the group at all.

Third, the distinction between subordinate helpers is possibly behavioral and physiological, but there is no guarantee of either. Physiologically, there may be hormonal differences between the two types of helpers, but such differences are generally transient consequences of status, rather than predictive (Schoech et al. 2004).

Fourth, although many studies, including that of white-browed scrubwrens, refer to helpers based on their status as subordinate to a dominant breeder, behavioral subordination is not, in general, a reliable means of distinguishing different kinds of helpers. Indeed, behavioral dominance may or may not be evident in a particular system, and even if it is, there is no guarantee that it will correspond to breeding status. For example, in superb fairy-wrens, males that have acquired dominant status do not mate with the dominant female when she is their mother (Chapter 8).

Fifth and last, subordinate helpers are not necessarily distinguishable on the basis of sex. Thus far we have used subordinate males to illustrate our points, and male helpers are generally more common than female helpers, at least in birds. But either or both can be subordinate helpers in some systems, and when the latter is the case, the criteria we propose to distinguish different kinds of helpers are likely to be the same (Koenig et al. 1998).

The distinction among helpers is critical for recognizing what factors are important to test in a particular system. When helpers are constrained from breeding

by incest avoidance, current and future indirect fitness benefits are a priori likely to be important to why they help. The importance of future direct fitness benefits to such individuals are also of interest to test, just as they would be for helpers that are not constrained from breeding within the group.

In contrast, subordinates that are *unrelated* to the opposite-sex breeder and therefore constrained by reproductive competition fall into at least three categories. Those that rarely or never reproduce while an auxiliary and are thus “nonbreeding helpers” may gain indirect fitness benefits if they are related to the dominant breeder of the same sex. Those that do reproduce – that is, share breeding status with the dominant, even if unequally, asynchronously, or infrequently – are breeders (or cobreeders) and should not be considered “helpers” at all. Finally, those that do not reproduce but are unrelated to the dominant breeders, as is the case for secondary helpers in pied kingfishers, clearly cannot gain indirect fitness benefits by helping. Such individuals are nonbreeding helpers, but are just as reasonably thought of as “hopeful breeders” whose behavior is driven by current or future direct fitness benefits.

What is problematic is when researchers confound the different types of helpers, several of which may be present in the same system. In particular, it is not novel or surprising to show that direct fitness benefits are important to “helpers” that are unrelated to the breeder of the opposite sex and that they share breeding status to some extent with the dominant of the same sex. Rather than reporting that such “helpers” have direct fitness benefits, authors of such studies should recognize that what they thought were helpers aren’t helpers after all. Reviews emphasizing the importance of direct fitness benefits to the evolution of helping behavior are potentially misleading unless the type of helper is clearly defined (Clutton-Brock 2002; Riehl 2013; Kingma et al. 2014).

Extra-group mating, high mortality, and incest

There are three nuances with regard to the above generalizations that we will consider in more detail.

Extra-group mating

In general, extra-group mating does not alter our conclusions, even when it is frequent. Animals do not necessarily know what we as researchers are now able to determine from molecular analyses, and although there may be exceptions, most appear to base their behavior on social criteria – that is, on the social mating system – rather than on the far more cryptic genetic mating system (see, for example, Chapters 2 and 3). Thus, the distinction made here between different kinds of subordinates is unlikely to be affected by the extent of extra-group parentage or other means by which parentage is obscured.

However, extra-group mating potentially confounds conclusions when the status of a particular individual is based *solely* on genetic data. For example, a subordinate female helper may be unrelated to the dominant breeder male and still function as if constrained by incest avoidance if she was the product of an extra-pair mating on the part of the dominant female. Analogously, a subordinate male helper that was “kidnapped” from a neighboring group (as described for pied babblers in Chapter 7, banded mongooses in Chapter 18, and white-winged coughts [*Corcorax melanorhamphos*] by Heinsohn [1991]) may nonetheless behave as if constrained from mating within the group by incest avoidance, despite being unrelated to either of the dominants. In such situations, kidnapping works because it takes advantage of the rules normally used to recognize and discriminate kin.

An additional consequence of extra-group mating is that it opens up a new path for direct fitness benefits by helpers that are otherwise constrained to be nonbreeders because of incest avoidance, reproductive competition, or both. Such a path to direct fitness can increase the potential for sexual selection (Webster et al. 1995), and provides an additional route to direct fitness benefits for helpers, especially if remaining in the natal group facilitates a male helper’s access to extra-pair matings.

Incest

The biggest difficulty with distinguishing the different types of subordinates arises when incest takes

place, since under such circumstances relatedness to the opposite-sex breeders by definition no longer constrains breeding. This is not true if incest is the incidental result of limited dispersal, which can bring unfamiliar kin into close proximity, in which case individuals, again basing their actions on social rather than genetic cues, are likely to behave as unrelated mates.

Given that one of the key criteria for distinguishing among subordinates is based on incest avoidance, it is unsurprising that our categorization of helpers breaks down when incest occurs. Fortunately, the frequency of incest in vertebrates, in both cooperative and non-cooperative breeders, is generally quite low (Rowley et al. 1993; Koenig and Haydock 2004), with banded mongooses and naked mole-rats being the only two species currently known that exhibit a mating system of facultative incest.

Adult mortality

High adult mortality and turnover are demographic factors that reduce relatedness and the indirect fitness benefits of helping behavior (Riehl 2013). However, as illustrated in Figure 20.1b and discussed in the context of family dynamics more generally by Emlen (1995, 1997), adult turnover and replacement is a key route by which one type of “helper” can transition to another (e.g., related to unrelated) or, more importantly, transition to breeding (or cobreeding) status. For example, a nonbreeding helper male in the acorn woodpeckers, whose parent of the opposite sex has died and been replaced by new, unrelated immigrants, can be viewed as “inheriting” cobreeding status and will subsequently breed (at least potentially) alongside his brother or father (Chapter 13), leading to questions about his relative benefits as a cobreeder, and render discussion of his benefits as a helper superfluous.

Recommendations

Any individual that provisions or otherwise assists in the raising of an offspring that is not his or her own has been defined as a helper (Brown 1987), but failing to distinguish among such individuals based on the factors limiting their reproduction is likely to result in

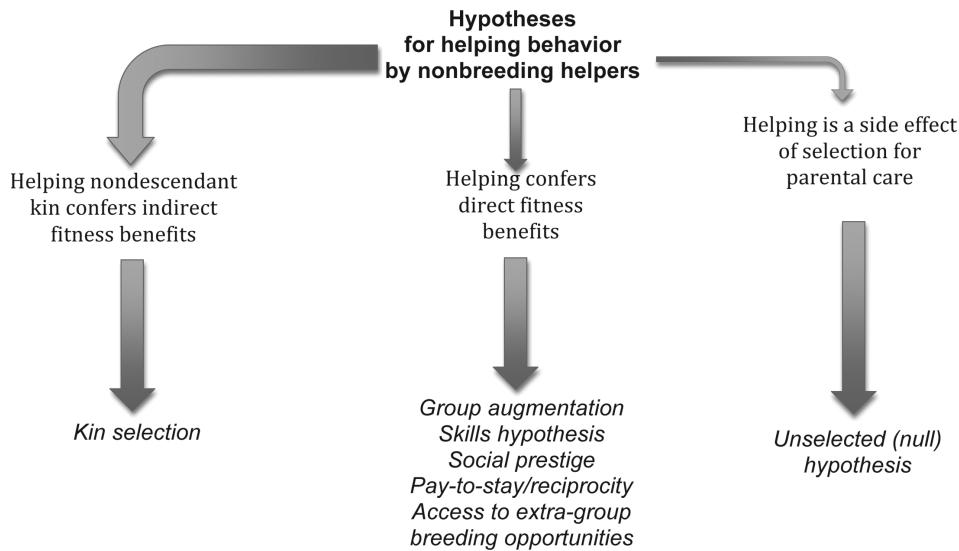


Figure 20.2. Hypotheses potentially selecting for helping behavior by nonbreeding helpers (offspring in the situation illustrated by Figure 20.1a that are constrained from breeding by incest avoidance). Indirect (kin selected) benefits are generally very important; direct fitness benefits may be significant but have rarely been confirmed. No recent authors support the null hypothesis that helping behavior is an unselected side effect of selection for parental care.

misinterpretation as to the significance of their role in the group. This is particularly important with respect to claims that “helpers” gain current direct fitness benefits (i.e., reproduce within their natal group), since such cases nearly always refer to individuals that have inherited breeding status due to turnovers and are thus no longer helpers at all, but rather cobreeders. Considering them to be helpers can lead to the erroneous conclusion that kinship is not important to helping, rather than viewing helping as a route to independent breeding within the group (i.e., future direct fitness benefits). As already discussed, such turnovers can be relatively common.

For the remainder of this chapter, “nonbreeding helpers” (or just “helpers”) will refer *only* to the first type of helper discussed: individuals that provide assistance in raising young, none of which is their own offspring, and are constrained from breeding due to incest avoidance. Individuals that are constrained from breeding by reproductive competition may or may not actually breed, and thus it will generally be prudent to avoid referring to such individuals as “helpers” unless

it is known that they rarely if ever successfully parent offspring. (Such absolute skew occurs, for example, in western bluebirds [Chapter 2], where no brothers or sons that help have yet been found by genetics to cobreed.) Even if they do not cobreed, new questions may arise from distinguishing them from nonbreeding helpers constrained by incest avoidance.

Evolution of helping behavior

Now that we have defined what we mean by a helper, let’s consider what they do – specifically their helping behavior – and why (Figure 20.2). The presence of nonbreeding helpers has almost always been found to benefit the individuals they assist in some way, either by facilitating the production of more young or by allowing breeders to lessen their breeding effort, generally by reducing their provisioning (“load-lightening”; Heinsohn 2004). In several cases, including superb fairy-wrens (Russell et al. 2007), carrion crows (*Corvus corone*; Chapter 6), and

Neolamprologus pulcher (Chapter 16), helping allows breeder females to lay smaller, and in the case of fairy-wrens, lower-quality, eggs.

Thus, given that helpers (as we have just restricted them) are assisting putative relatives, indirect fitness benefits – those gained by assisting in the production of nondescendant kin – are likely to be important to helping behavior in all species where helping is found, a conclusion further bolstered by evidence of kin recognition and kin discrimination, which have been found to be important in several of the species covered in this book. What is not always clear is whether observed benefits are a result of helping per se rather than a by-product of helpers being in the group (e.g., a group size effect) – a critical assumption that is easily overlooked. Nonetheless, the benefits associated with helpers, along with the variability in helping behavior frequently associated with relatedness and evidence that helping is costly (Heinsohn and Cockburn 1994; see also Chapter 17), counters the hypothesis that helping behavior is an “unselected” phenomenon (Craig and Jamieson 1990).

Paradoxically, however, attempts to quantify kin-selected benefits of helping by nonbreeding helpers have often revealed that they are small relative to what the same individual would be expected to gain by breeding independently; this is, for example, the case in western bluebirds and long-tailed tits (Chapters 2 and 3). Along the same lines, the high incidence of extra-pair fertilizations in superb fairy-wrens means that initial estimates of the inclusive fitness benefits gained by helpers in this species were considerably optimistic (Chapter 8).

In contrast to strong evidence for at least some indirect fitness benefits, evidence that the provisioning behavior of helpers confers direct fitness benefits through mechanisms such as reciprocity (“pay-to-stay”), social prestige, the “skills hypothesis,” or group augmentation remains scarce (Dickinson and Hatchwell 2004; Chapter 10), despite attempts to explicitly test for such phenomena in western bluebirds (Chapter 2), red-cockaded woodpeckers (Chapter 4), chestnut-crowned babblers (Chapter 9), bell miners (*Manorina melanophrys*; Chapter 10), and acorn woodpeckers (Chapter 13). Again, distinguishing between the different kinds of subordinates is important, as

illustrated by Seychelles warblers, where earlier work indicating that helping behavior conferred experience, allowing birds to be more successful in their first breeding attempt, turns out to be confounded by the finding that many of the “helpers” were most likely subordinate cobreeders (Chapter 12).

Two cases in which researchers have found an important role for direct fitness benefits are worth mentioning. First is the superb fairy-wren, where experiments suggest that dominants coerce helpers into helping by punishing them when they are temporarily removed from the territory to simulate defection (Mulder and Langmore 1993). Such experiments sorely need repeating in order to demonstrate not only that helpers are punished when they fail to help, but that aggression causes “lazy” individuals to increase their helping behavior (Raihani et al. 2012). The second is *Neolamprologus pulcher*, where detailed experimental work by Taborsky and his colleagues has demonstrated that pay-to-stay is an important mechanism by which helpers are allowed to remain in groups (Chapter 16). Note, however, that although delayed dispersal occurs and some subordinates are related in this species, breeding turnovers are common and thus a majority of subordinates are no longer helpers as we have defined them above, but likely to be aspiring, at least at some level, to breeding status within the group.

The evolutionary origins of cooperative breeding

The most general hypothesis in the category of evolutionary origins is the “life-history” hypothesis, which proposes that low annual mortality predisposes lineages to exhibit delayed dispersal and cooperative breeding by driving low territory turnover and thus strengthening ecological constraints (Arnold and Owens 1998, 1999; Figure 20.3). This hypothesis is supported by evidence that the incidence of cooperative breeding within families of birds is associated with decreases in annual adult mortality and modal clutch size, and that the proportion of cooperatively breeding species per family is correlated with a low family-typical value of annual mortality. Arnold and

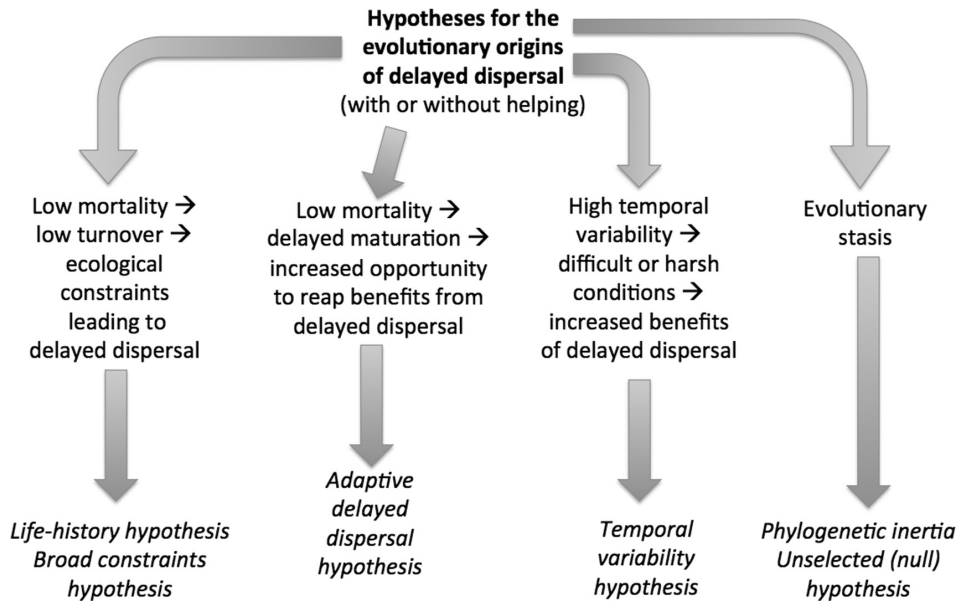


Figure 20.3. Hypotheses for the evolutionary origins of delayed dispersal with or without helping behavior.

Owens (1998) interpreted these results as indicating that low mortality predisposes cooperative breeding rather than vice versa.

Two aspects of this hypothesis are worth noting. First, being phylogenetically based, it is at a different level of analysis and thus does not refute the functional-level explanations we discuss later. Second, although its primary focus is on the life-history factors that predispose a population to evolve delayed dispersal and cooperative breeding, it involves an ecological component, specifically that the life-history trait of high longevity drives strong demographic constraints in the form of high competition for relatively few breeding opportunities in the population (Rowley and Russell 1990).

Related to the life-history hypothesis are the “broad constraints” hypothesis of Hatchwell and Komdeur (2000) and the “adaptive delayed dispersal” hypothesis of Covas and Griesser (2007). Both accept the importance of low mortality rates and go on to postulate that this trait works in conjunction with ecological factors to predispose certain lineages in the direction of cooperative breeding. Hatchwell and Komdeur (2000) stress the importance of a suite of life-history factors working

in conjunction with each other to facilitate constraints and delayed dispersal, while Covas and Griesser (2007) focus on how life-history factors associated with cooperative breeding might interact with various benefits of philopatry to enhance offspring survival and lead to the situation where parents gain by having young stay – that is, to mutual benefits of delayed dispersal outweighing the costs.

One other hypothesis that we place in the category of evolutionary origins is the “temporal variability” hypothesis (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011; Chapter 11), which proposes that high temporal variability predisposes lineages to exhibit cooperative breeding by setting the stage for strategies that maximize the social benefits of delayed dispersal and group living when conditions are poor. In contrast to the other life-history hypotheses, however, the temporal variability hypothesis puts the ecological component first, identifying it as the driver of the key life-history traits that are associated with cooperative breeding rather than vice versa.

Finally, the null hypothesis for the evolutionary origins of delayed dispersal and cooperative breeding is the

“phylogenetic inertia” hypothesis put forth by Edwards and Naem (1993). This hypothesis proposes that cooperative breeding is not driven by any specific life history or ecological driver, but is the consequence of evolutionary stasis resulting in the retention of these traits in certain lineages. As with any evolutionary null hypothesis, it can only be tested by the elimination of alternatives.

Ecological factors and the evolution of delayed dispersal

We now turn to the particularly vexing and contentious question of what ecological factors are important to the evolution of delayed dispersal by nonbreeding helpers. Everyone, we believe, can agree that delayed dispersal, which does not inevitably go along with helping (Chapter 1), occurs when two criteria are met. First, the average lifetime benefit gained by an individual remaining in its natal group is greater than or equivalent to the benefit of dispersing and trying to achieve an independent breeding position; and second, the average lifetime benefit to the dominant breeders of allowing those offspring to remain and, at least potentially, help is greater than or equivalent to the benefit of forcing them to disperse. (All alternatives are assumed to take into consideration the inclusive fitness costs of the behavior as well as the benefits.) Measuring these costs and benefits, especially in terms of lifetime fitness, is difficult and one reason why long-term studies are so vital.

Beyond these somewhat obvious (as well as onerous) conditions, there are several assumptions that we believe are important to embrace in order to understand delayed dispersal. First, given any particular ecological circumstance, it is always better to breed than to be a nonbreeding helper. Consequently, if nonbreeding helpers exist, it is at least in part because of some constraint on their ability to breed.

Second, constraints are universal, and thus simply acknowledging the existence of constraints on dispersal and independent breeding does little to illuminate the ecological drivers of these phenomena. There are, however, different kinds of constraints that vary in their relative strength depending on ecological, environmental,

and social circumstances. Thus, despite their ubiquity, identifying the constraints important in a particular system is an important part of understanding the ecological drivers of delayed dispersal.

Third, the benefits of delayed dispersal, like the benefits associated with any kind of group living, are not automatic (Alexander 1974). There are, however, a wide variety of social benefits that potentially become available to individuals that delay dispersal or disperse locally and maintain proximity to kin, one of which is the potential to provision or otherwise help and be helped by close relatives.

Fourth, there are exceptions to almost any generalization that is made concerning delayed dispersal and cooperative breeding. Our goal here is to organize and frame our knowledge about these phenomena in a way that is conceptually useful and applicable to a large proportion of cases. We have tried to cast our thoughts as generally as possible, but they are nonetheless unlikely to apply to every species or every situation.

Based on these postulates, we propose that the ecological factors important to delayed dispersal are profitably visualized as a continuum. The inability to breed independently is important for all species that exhibit delayed dispersal; what varies more widely is the degree to which they are able to accrue the potential benefits associated with continued access to the natal group or the natal territory. When such benefits are small, ecological factors constitute the main limits on opportunities to breed independently from the natal group; we call these “resource constraints” since most authors envision them as involving access to a resource such as a cavity, territory, or mate. When benefits of being in a group are large, reproductive competition and other social factors are likely to limit opportunities to reproduce, both within or outside the natal group; we refer to these as “social benefits,” but they can just as plausibly be thought of as “social constraints,” as we discuss below in the section “Constraints and benefits act in concert to favor cooperative breeding.”

At one end of the cooperative-breeding continuum where the net benefit of delayed dispersal and helping is low, delayed breeding is primarily driven by shortage of resources, mates, or breeding space. Helpers are “making the best of a bad job” and the natal territory

is the best place to wait for breeding opportunities. At the other end are species for which the relative benefit associated with delayed dispersal is considerable and delayed reproduction is driven by social constraints or social competition. Delayed dispersal in such species can reasonably be thought of as being driven by the benefits of philopatry and the critical importance of socially produced benefits such as helping behavior. Although authors often stress factors falling into one end or the other of this continuum, constraints and benefits can be detected in nearly all cooperative breeding systems (Table 20.1).

Constraints-based systems

Constraints on access to resources

Resource-access constraints postulate that the key factor driving delayed dispersal and cooperative breeding is access to some resource that limits the ability of individuals to breed successfully, and, in addition, their potential to leave and become “floaters” in the population (Koenig et al. 1992). In some cases the limiting resource is a breeding territory, but it can also be an engineered resource such as the roosting cavities of red-cockaded woodpeckers (Chapter 4), the granaries and nesting cavities of acorn woodpeckers (Chapter 13), or, to the extent that it is farmed by the birds that live on a site over many generations, the mistletoe that serves as winter food for western bluebirds (Chapter 2). The key is that restricted access to the resource is the primary constraint increasing the costs of dispersal to such an extent that individuals are better off remaining on their natal territory, and, at least potentially, helping to raise younger siblings, rather than assuming the costs of floating or dispersing into a situation where obtaining the resources necessary for breeding is unlikely and their survivorship low. Benefits of helping, while potentially small, still provide indirect fitness advantages compensating for being, at least temporarily, unable to breed.

The fundamental characteristic of cooperative breeders in this category is that the inclusive fitness of a

helper is less than what the same or a comparable individual would achieve by breeding in the absence of the limitation. In the absence of such a test or comparison, an alternative prediction is that the per capita reproductive success of groups is less than that of unaided pairs (Koenig 1981; see also Chapter 14). Such comparisons are not conclusive, even when confounding factors such as experience, territory quality, and group composition are carefully controlled. But in many cases, comparing the per capita reproductive success of groups versus pairs can provide a useful and often underappreciated starting point for further investigation of the ecological drivers of delayed dispersal and cooperative breeding.

The idea of constraints driving delayed dispersal has frequently been called the “ecological constraints” hypothesis; however, given the ubiquity of constraints, this term should be used with caution. Cooperative breeders that face resource constraints are typically territorial and live in relatively small groups, and when the limiting resource appears to be space or suitable territories (see, for example, Chapter 5), constraints arguments imply that all suitable territories are occupied and thus that cooperative breeding is driven by “habitat saturation.” This latter term is also fraught with problems (Koenig et al. 1992), but is nonetheless useful for conveying the idea that individuals that stay home are making the best of a bad job because of their inability to compete successfully for a suitable breeding territory or space encompassing sufficient resources to breed.

A corollary of the prediction that the inclusive fitness of a helper is less than what could be achieved by breeding in the absence of the limitation is that helpers should attempt to disperse when given access to a suitable territory or limiting resource. Empirical evidence for this prediction comes from Florida scrub-jays (Chapter 5) and acorn woodpeckers (Chapter 13), where birds regularly fight to fill reproductive vacancies. Experimental evidence exists for red-cockaded woodpeckers (Chapter 4), where helpers quickly disperse and colonize artificial cavities when they are provided, and Seychelles warblers (Chapter 12), in which birds transplanted to uninhabited islands forgo group

Table 20.1. The primary factors driving sociality and cooperative breeding in the species discussed in this volume

Species	Key benefits of delayed dispersal or group living	Key constraints to natal dispersal and/or independent breeding	Comments
Siberian jay	Nepotism (access to food and protection against predators); natal territory a safe haven	High-quality territories (unthinned spruce forest) limited	Delayed dispersal but no helping
Western bluebird	Access to mistletoe and reduced aggression by mothers	Female mates	Redirected helpers common; adult helpers all males; simultaneous breeder-helpers occur
Long-tailed tit	Communal roosting	Short breeding season with very high nest predation; seasonal decline in reproductive success	All helpers failed breeders; 85% are males
Florida scrub-jay	Access to year-round food, enhanced juvenile survival and dispersal opportunities	Habitat saturation; limited post-fire successional habitat	Intense competition for unusually large territories in habitat-limited, fire-prone ecosystem
Red-cockaded woodpecker	Living on or acquiring a high-quality territory	Roosting and nesting cavities	Experimental support for importance of cavities
Carrion crow	Nepotism (access to food); natal territory a safe haven	Shortage of territories constrains independent breeding	Differences between populations not due to differences in constraints
Southern pied babbler	Buffering against harsh conditions	Highly variable conditions	"Kidnapping" of helpers; groups merge during droughts
Superb fairy-wren	Access to within- and extra-group reproduction	Female mates	Experimental support for shortage of females
Chestnut-crowned babbler	Reduced predation; thermoregulatory benefits of huddling	Inability to breed as a pair in most years	Obligate group living
Bell miner	Significant benefits of group sociality; breeding positions for males only within natal coterie	Collective food resource defence (against allospecifics); possibly collective anti-predator defence	Live in large colonies divided into coterie; complex helping patterns; kin-selected helping crucial
Superb starlings	Reduced fecundity variance; increased offspring provisioning and enhanced nest defense	Highly variable conditions and heterogeneous landscape	Obligate group living; bet-hedging important
Seychelles warbler	Access to high-quality territories; higher survival; higher future reproductive success; both direct and indirect benefits	Saturation of high-quality habitat	Experimental evidence for importance of high-quality territories
Acorn woodpecker	Some indirect fitness benefits for helpers	Nesting cavities and acorn-storage facilities	Intense competition for reproductive vacancies expressed through "power struggles"
Taiwan yuhina	Lower parental cost of nesting in a harsh environment	High nest failure risk due to predation and severe weather	Non-kin based groups

(cont.)

Table 20.1 (*cont.*)

Species	Key benefits of delayed dispersal or group living	Key constraints to natal dispersal and/or independent breeding	Comments
Guira cuckoo	Indirect fitness and reduced competition in kin-based groups; enhanced foraging and protection against predators	Reproductive competition intense	No apparent habitat saturation; egg ejection and infanticide common
<i>Neolamprologus pulcher</i>	Protection against predation; participation in reproduction	High predation pressure	Obligate group living; cooperation payment for being allowed to stay in the group
Meerkat	Enhanced survival and increased chance of breeding	Absence of unrelated mates for males; reproductive suppression by dominant for females	Obligate group living
Banded mongoose	Enhanced competitiveness; protection against predation	Intergroup competition	Obligate group living; "kidnapping" of offspring
Naked mole-rat	Protection against predation and reduced risk of unsuccessful foraging	Harsh environmental conditions	Obligate group living; aridity food distribution hypothesis

living until the population increases to the point that high-quality territories are occupied and the habitat is again saturated.

One of the long-recognized difficulties with the concepts of ecological constraints and habitat saturation is that they do a poor job of distinguishing cooperative breeders from noncooperative species. One attempt to make such a distinction was the "marginal habitat" hypothesis, which suggests that delayed dispersal results from a shortage of suboptimal habitat or territories, thus producing relatively many offspring fledging from high-quality territories that have few options to disperse to territories of lesser quality (Koenig and Pitelka 1981). This idea was subsequently turned around by Stacey and Ligon (1991) in a paper hypothesizing that even when territory quality varies continuously, rather than declining precipitously, high variance in territory quality can drive delayed dispersal and cooperative breeding. Following Doerr and Doerr (2006), we call this the "variance" hypothesis.

Regardless of the validity of these hypotheses as ways to envision the specific ecological conditions potentially facilitating delayed dispersal in different populations, neither has thus far been particularly useful empirically, in part because quantifying the

complete distribution of territory quality within or between populations is challenging (but see Chapter 2 for a within-population example). Meanwhile, despite some advances (Cockburn and Russell 2011; Jetz and Rubenstein 2011), our ability to predict interspecific differences in cooperative breeding beyond a clear relationship with sedentariness (Arnold and Owens 1999) remains poor (Cockburn 2014), and is clearly an area in which significant progress stands to be made in the future.

Shortage of mates

Whether or not resource constraints are important in a population, independent breeding can be limited by a shortage of available mates (Chapter 2). A landmark experiment on superb fairy-wrens demonstrated that both territories and mates are important constraints on independent breeding in this species (Pruett-Jones and Lewis 1990). When breeder males were removed, helpers moved in to replace them within hours; when both members of a pair were removed, replacement did not take place until the female was returned to the territory two to three days later. Further discussion of this example is provided by Cockburn et al. (Chapter 8), who point

out some of the difficulties of generalizing it to other fairy-wren species.

Benefits-based systems

Socially produced benefits and the hard-life hypothesis

Where the benefits associated with delayed dispersal and helping augment fitness, remaining in the group is potentially superior to breeding independently. Such social benefits may be produced through nepotism (Ekman et al. 2004), parental facilitation (Brown and Brown 1984), the “safe-haven” effect of living on a high-quality and familiar territory (Kokko and Ekman 2002), or an enhanced potential for inheriting the territory in the future and becoming a breeder. In more extreme (and presumably derived) cases, benefits may consist largely of the indirect fitness coming from provisioning kin or group augmentation, which involves helpers later being assisted by group members (often kin) that were added as a function of their help (Kokko et al. 2001; Kingma et al. 2014). As suggested by Russell in Chapter 9, such cases may be distinct in that helping behavior has become so important that it is driving delayed dispersal rather than (as is more commonly envisioned) the reverse.

Benefits-based hypotheses propose that the key constraint leading to delayed dispersal is not gaining access to suitable space or a mate, but rather the ability to survive and breed successfully independent of a group despite access to other critical resources. Species for which delayed dispersal is benefits-based often live in relatively large aggregations or colonies comprised of a mix of kin and nonkin. Often, the benefit driving delayed dispersal in such cases is socially produced, specifically the presence of additional individuals and/or the availability of potential helpers from within the group or colony. In such cases, the group itself is in effect the resource limiting the ability of individuals to breed on their own.

The fundamental characteristic of benefits-based cooperative breeding is that the mean inclusive fitness benefits of delayers increase with group size up to some

empirical maximum greater than the mean for a pair of individuals. Examples where such social benefits are likely to be important include species in which high predation risk has resulted in the evolution of sophisticated babysitting and sentinel systems such as in pied babblers (Chapter 7), meerkats (Chapter 17), and banded mongooses (Chapter 18). Striking evidence of such social benefits is provided by the phenomenon of “kidnapping” young from neighboring groups, as found in the babblers and mongooses.

Intuitively, the most straightforward benefits-based hypothesis is that successful breeding is so difficult that it cannot be accomplished by a pair of individuals alone, but rather can be done only by cooperative groups of individuals (Emlen 1982), an idea that has been referred to as the “hard-life” hypothesis (Koenig and Mumme 1987; Koenig et al. 2011). The importance of large group sizes for successful breeding need not be this extreme, however, and the hard-life hypothesis is potentially applicable to any case in which the difficulties of breeding successfully are mitigated by additional help to an extent that helping compensates for the loss in fitness helpers forgo by not breeding independently. Such conditions may only occur intermittently as in populations subject to conditions that vary dramatically from year to year, leading to helpers having very different effects from year to year and breeding group sizes that vary depending on the ecological circumstances.

Benefits of philopatry

Starting with Stacey and Ligon (1987, 1991), “benefits of philopatry” has been used in two very different ways. First, it is often used in the sense of *any* benefit gained by individuals living in a cooperative, breeding group, whether or not those benefits outweigh the advantages of independent reproduction. Second, the term is also used to refer to the variance hypothesis, as described earlier.

These two concepts are, however, distinct. Stacey and Ligon’s focus on variance in territory quality leads to the important general point that the costs and benefits of dispersal compared to independent reproduction can

differ among individuals based on their relative options. Variance in territory quality as a particular kind of condition potentially facilitating delayed dispersal should not, however, be conflated with the more general use of “benefits of philopatry” to describe the many ways individuals of a particular species benefit from delayed dispersal. Just as all cooperative breeders are subject to constraints, most accrue at least some benefits from delayed dispersal and helping behavior. In other words, virtually all cooperative-breeding species gain some “benefits of philopatry,” regardless of whether delayed dispersal is primarily constraints-driven or benefits-driven.

Bet-hedging and environmental variability

Another potentially important benefits-based hypothesis is that cooperative breeding is a bet-hedging strategy (Rubenstein 2011) selected for because the reduced (arithmetic) mean fitness suffered by helpers is more than compensated by a decrease in fecundity variance through time (Starrfelt and Kokko 2012). Thus, both bet-hedging and the hard-life hypotheses propose that delayed dispersers gain significant inclusive fitness benefits potentially outweighing those of independent breeding, the difference being whether the benefit results from lifetime increases in inclusive fitness (hard-life hypothesis) or reduced fecundity variance (bet-hedging). Bet-hedging has been proposed to be important to cooperative breeding in superb starlings (Chapter 11); its potential importance to other cooperative breeders remains to be determined, however (Koenig and Walters 2015).

Benefits-based hypotheses in general, and the hard-life and bet-hedging hypotheses in particular, propose that delayed dispersal and cooperative breeding are favored by harsh, variable, and unpredictable conditions (Emlen 1982; Rubenstein 2011). To the extent that this is the case, a prediction of benefits-based hypotheses is that helpers should have a greater effect on reproductive success when conditions are poor than when they are good, a result found in several cooperatively breeding species (Magrath 2001) including pied babblers (Chapter 7), superb starlings (Chapter 11) and grey-capped social weavers (S. T. Emlen, unpubl. data),

as well as sociable weavers, *Philetairus socius* (Covas et al. 2008) and white-fronted bee-eaters, *Merops bullockoides* (Emlen 1990; Emlen and Wrege 1991). Surprisingly, the opposite result is observed in acorn woodpeckers: helper males have a greater effect on reproductive success following good, rather than poor, acorn crops (Koenig et al. 2011; Chapter 13).

When conditions vary greatly among individuals or from one year to the next, a potential response is plasticity and the ability to switch between delayed dispersal and independent breeding as conditions permit. Such fluid moving back and forth between helping and breeding independently also occurs in species that live in kin neighborhoods, suggesting that understanding the ecological drivers of more dispersed aggregations of kin could provide new insights into where such species fit on the constraints/benefits-based continuum.

Obligate cooperative breeding

Benefits-based delayed dispersal is most evident in obligate cooperative breeders – species in which individuals are always or nearly always found in groups, including chestnut-crowned babblers (Chapter 9), bell miners (Chapter 10), meerkats (Chapter 17), banded mongooses (Chapter 18), and mole-rats (Chapter 19). Although constraints are, as usual, important to delayed dispersal in such species, the social benefits of delayed dispersal and living in a group clearly outweigh the costs of independent breeding. In the chestnut-crowned babblers, it is further hypothesized that the benefits associated with helping per se are sufficient to explain delayed dispersal (Chapter 9), a possibility that had previously been thought to be rare (Ekman et al. 2004).

Constraints and benefits act in concert to favor cooperative breeding

One lesson from the studies summarized in this book is that it is challenging to categorize and distinguish cooperative breeders based on ecological constraints and benefits of philopatry, since both are frequently, and perhaps typically, important (Table 20.1). While the field has emphasized these as distinct causal

factors, ecological constraints are not unique to cooperative breeders; indeed, it is not even obvious that constraints are greater for cooperative breeders than for noncooperative species (Hatchwell and Komdeur 2000). More useful is to focus on how the net benefit of helping for parents and their offspring compares with outside options and why in cooperative breeders this differential leads to delayed dispersal and helping.

An illustrative example is that of the importance of the natal territory as a safe haven for Siberian jays (Chapter 1). In this species, offspring commonly delay breeding and those that also delay dispersal reap nepotistic benefits, surviving longer and having higher lifetime reproductive success compared to immigrants that have joined their group as nonbreeders. Nonetheless, these benefits of philopatry are not necessarily the primary reason why young Siberian jays delay dispersal and fail to breed independently. Instead, a key factor is the limited availability of high-quality breeding sites, which constrains the ability of young to breed for up to three years. Delayed dispersal in this species is driven importantly by ecological constraints, but the natal territory is the best place for offspring to wait for the opportunity to breed, largely due to nepotism. Similar issues involving both constraints and benefits can be identified for many, if not all, the species considered in this book (Table 20.1).

This point is particularly evident in obligate cooperative breeders; indeed, constraints and benefits are arguably indistinguishable in such cases. Consider naked mole-rats (Chapter 19). The currently accepted hypothesis for natal philopatry, cooperative breeding, and ultimately the evolution of eusociality in this species is the “aridity food distribution hypothesis,” which proposes that the suite of characters that comprise the cooperative breeding syndrome have evolved in response to the hardness of the soil, the costs of making new burrows, and the risks associated with foraging and dispersal. These factors can clearly be considered resource constraints that render it difficult for individuals to disperse and obtain a breeding position. Just as reasonably, however, the existence of a burrow system for safe foraging and safe living are benefits associated with group-living that make it impossible for

individuals to breed successfully on their own even if they disperse to a suitable site.

As these examples show, the dichotomy that has frequently been made in the literature between benefits of philopatry and ecological constraints is a red herring; constraints and benefits act in concert to shape cooperative breeding systems and to produce the variety of social systems described in this book. This does not mean that we cannot draw any generalizations, but it argues for a pluralistic approach to investigation of the drivers of cooperative breeding that is less linear and more complex than previously acknowledged.

What are the outside options?

Few studies have provided insights on the benefits of remaining in the natal group relative to floating or dispersing to another group in which to live. One example where such options have been examined is that of the Siberian jay, where young birds exhibit higher survival when they remain on their natal territory than when they join new groups (Chapter 1). In contrast, overwinter survival of first-winter male western bluebirds is strikingly high (95%) whether they remain on their natal territory or disperse locally, leading to the hypothesis that males dispersing locally distribute themselves in a way that approximates an ideal-free distribution across habitat that is generally of high quality (with respect to overwinter survival), but that habitat quality varies importantly at the landscape scale (Chapter 2).

At least as important as the relative costs and benefits of delayed dispersal to offspring are the costs and benefits to parents, which are generally assumed to have the ability to either tolerate offspring or evict them. This is an area where additional field studies could contribute significantly and where insights may arise with new models that vary the level of parental control and treat delayed dispersal as an interaction between parents and offspring in which fitness effects on both can vary. Particularly exciting are new tracking technologies that promise to transform what we know about dispersal and the poorly understood period between fledging and first breeding (Koenig et al. 1996). Such methods will allow researchers to measure the fitness of dispersers, and equally importantly, floaters, whose fitness is

likely to play a vital role in understanding why animals remain near home and/or near kin.

Delayed dispersal is not a prerequisite for kin-based cooperative breeding

Although delayed dispersal and helping are commonly associated, studies of western bluebirds (Chapter 2) and long-tailed tits (Chapter 3), and acorn woodpeckers (Chapter 13) illustrate that delayed dispersal is not a necessary precursor to kin-based helping behavior. In western bluebirds, males settle near kin in both migratory and resident populations, all but a few offspring disperse to breed, and helping appears to be making the best of a bad job due to a shortage of females or loss of a mate midseason (Chapter 2). In long-tailed tits, all offspring disperse, but many remain in the vicinity of their natal site and subsequently have the opportunity to help at the nests of relatives when their own nests fail, which they often do (Chapter 3). Helping in this species is compensated by future indirect fitness benefits that arise when helpers lighten the workload of male relatives they assist (Meade et al. 2010). Last but not least, a significant fraction of acorn woodpeckers inheriting their natal territory do so *after* dispersing and attempting to breed elsewhere (Chapter 13). In all three of these cases, opportunities to help are provided by remaining in close proximity to kin, and thus further exploration of the selective factors, both social and otherwise, of maintaining close proximity to kin is clearly needed.

Where to go from here

The four factors important to the decision of an individual to delay dispersal are: (1) the constraints limiting outside options; (2) the benefits of group living; (3) relatedness to other individuals in the group in which the individual stays or potentially interacts; and (4) whether they are tolerated by the dominant group members. Of these factors, relatedness can now be determined with some precision using a combination of social genealogies and molecular techniques or, more coarsely, with molecular techniques alone. The benefits of group living have been investigated in many

species, but numerous questions remain concerning the kinds of fitness benefits helpers may be gaining in different systems. As for the constraints limiting outside options such as floating or settling in groups of nonkin, we know strikingly little in most cases. We have a similarly poor understanding of what ecological factors prompt parents in some species to tolerate the continued presence of their offspring.

Drilling into the details of such factors is one of the great benefits of a system such as *Neolamprologus pulcher*, on which experiments can be conducted under relatively realistic conditions in the laboratory (Chapter 16). For the other species in this book, we can only hope that continued long-term studies combined with emerging technologies will begin to fill this gap by allowing workers to follow individuals and quantify the fitness consequences of their behavior as they engage in pursuing options that up until now have been challenging to observe. We expect that a hypothetical third volume in this series, published in another 25 years, will have much to say about the costs and benefits of alternative strategies in ways that we can only dream about today.

It is also worth noting that the four factors we have identified as key to delayed dispersal above are essentially the same factors determining reproductive partitioning in optimal skew models (Keller and Reeve 1994). Such models have already been adapted to address the issues of delayed dispersal and living in kin neighborhoods (Stern 2012). Of course, many of the same issues that have made it difficult to test skew models using empirical data on reproductive sharing (Magrath et al. 2004) are likely to apply to testing similar types of models for delayed dispersal. Nonetheless, such modeling efforts have the potential to add significantly to, and help guide, future empirical work in the field of cooperative breeding.

Unanswered questions

This synthesis discusses only a small set of the unanswered questions raised by the studies of cooperative breeding included in this book. Consider the variability in the levels of extra-group paternity observed in cooperative breeders, which range from near zero in

the Florida scrub-jay (Chapter 5) to 61% in the superb fairy-wren, possibly the most genetically promiscuous, socially monogamous species in existence. Some hints as to what might be driving such variability can be gleaned from chapters here: for example, Cockburn et al. (Chapter 8) make a strong case for how sexual selection drives the frequency of extra-pair fertilizations in fairy-wrens, and Dickinson et al. (Chapter 2) point to how extra-pair fertilizations favoring older males can potentially augment delayed fitness benefits and thus favor helping. Nonetheless, our understanding of such variation remains poor.

Another notable problem has to do with the considerable variability in cooperative behavior exhibited by helpers, which in at least some species range from individuals providing more help than do the breeders themselves to helpers that apparently devote little or no effort to cooperative activities (Chapter 9). Although some of the variation is attributable to genetic relatedness, or in some cases need (Chapter 6), much remains unexplained, and the evolution of such “flexible parenting” (or, in this case, “flexible alloparenting”), within a class of individuals that otherwise seem to be similar, is a problem that has only recently begun to be explored (Brouwer et al. 2014; Royle et al. 2014). Our suggestions for differentiating helpers from potential cobreeders will hopefully help workers address this problem using increasingly informative comparison groups in the future.

At the very least, one issue all workers in this field can probably agree on is that much work remains to be done, and that the primary innovations in this field are likely to come from the kinds of long-term studies highlighted in this book. We hope that the chapters in this book will help pave the way for future workers to reveal answers to the many unresolved issues in this field, which we expect to continue to excite behavioral ecologists through the end of the twenty-first century and beyond.

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REFERENCES

- Alexander, R. D. (1974). The evolution of social behavior. *Annu. Rev. Ecol. Syst.*, 5, 325–383.
- Arnold, K. E. and Owens, I. P. F. (1998). Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proc. R. Soc. London B*, 265, 739–745.
- Arnold, K. E. and Owens, I. P. F. (1999). Cooperative breeding in birds: the role of ecology. *Behav. Ecol.*, 10, 465–471.
- Boomsma, J. J. (2009). Lifetime monogamy and the evolution of eusociality. *Phil. Trans. R. Soc. London B*, 364, 3191–3207.
- Brouwer, L., van de Pol, M., and Cockburn, A. (2014). The role of social environment on parental care: offspring benefit more from the presence of female than male helpers. *J. Anim. Ecol.*, 83, 491–503.
- Brown, J. L. (1987). *Helping and Communal Breeding in Birds: Ecology and Evolution*. Princeton, NJ: Princeton University Press.
- Brown, J. L. and Brown, E. R. (1984). Parental facilitation: parent-offspring relations in communally breeding birds. *Behav. Ecol. Sociobiol.*, 14, 203–209.
- Clutton-Brock, T. H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, 296, 69–72.
- Cockburn, A. (2004). Mating systems and sexual conflict. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 81–101.
- Cockburn, A. (2014). Behavioral ecology as big science: 25 years of asking the same questions. *Behav. Ecol.*, 25, 1283–1286.
- Cockburn, A. and Russell, A. F. (2011) Cooperative breeding: a question of climate? *Curr. Biol.*, 21, R195–R197.

- Cornwallis, C. K., West, S. A., Davis, K. E., and Griffin, A. S. (2010). Promiscuity and the evolutionary transition to complex societies. *Nature*, 466, 969–972.
- Covas, R. and Griesser, M. (2007). Life history and the evolution of family living in birds. *Proc. R. Soc. London B*, 274, 1349–1357.
- Covas, R., Du Plessis, M. A., and Doutrelant, C. (2008) Helpers in colonial cooperatively breeding sociable weavers *Philetaurus socius* contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.*, 63, 103–112.
- Craig, J. L. and Jamieson, I. G. (1990). Pukeko: different approaches and some different answers. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*, ed. P. B. Stacey and W. D. Koenig. Cambridge: Cambridge University Press, pp. 385–412.
- Dickinson, J. L. and Hatchwell, B. J. (2004). Fitness consequences of helping. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 48–66.
- Dickinson, J. L., Koenig, W. D., and Pitelka, F. A. (1996). Fitness consequences of helping behavior in the western bluebird. *Behav. Ecol.*, 7, 168–177.
- Doerr, E. D. and Doerr, V. A. J. (2006). Comparative demography of treecreepers: evaluating hypotheses for the evolution and maintenance of cooperative breeding. *Anim. Behav.*, 72, 147–159.
- Edwards, S. V. and Naeem, S. (1993). The phylogenetic component of cooperative breeding in perching birds. *Am. Nat.*, 141, 754–789.
- Ekman, J., Dickinson, J. L., Hatchwell, B. J., and Griesser, M. (2004). Delayed dispersal. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 35–47.
- Ekstrom, J. M. M., Burke, T., Randrianaina, L., and Birkhead, T. R. (2007). Unusual sex roles in a highly promiscuous parrot: the greater vasa parrot *Caracopsis vasa*. *Ibis*, 149, 313–320.
- Emlen, S. T. (1982). The evolution of helping I. An ecological constraints model. *Am. Nat.*, 119, 29–39.
- Emlen, S. T. (1990). White-fronted bee-eaters: helping in a colonially nesting species. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 487–526.
- Emlen, S. T. (1995). An evolutionary theory of the family. *Proc. Natl. Acad. Sci. (USA)*, 92, 8092–8099.
- Emlen, S. T. (1996). Reproductive sharing in different types of kin associations. *Am. Nat.*, 148, 756–763.
- Emlen, S. T. (1997). Predicting family dynamics in social vertebrates. In: *Behavioural Ecology: An Evolutionary Approach*, 4th ed., ed. J. R. Krebs and N. B. Davies. Oxford: Blackwell, pp. 228–253.
- Emlen, S. T. and Wrege, P. H. (1991). Breeding biology of white-fronted bee-eaters at Nakuru: the influence of helpers on breeder fitness. *J. Anim. Ecol.*, 60, 309–326.
- Fessl, B., Kleindorfer, S., Hoi, H., and Lorenz, K. (1996). Extra male parental behaviour: evidence for an alternative mating strategy in the moustached warbler *Acrocephalus melanopogon*. *J. Avian Biol.*, 27, 88–91.
- Hatchwell, B. J. and Komdeur, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.*, 59, 1079–1086.
- Heinsohn, R. G. (1991). Kidnapping and reciprocity in cooperatively breeding white-winged choughs. *Anim. Behav.*, 41, 1097–1100.
- Heinsohn, R. G. (2004). Parental care, load-lightening, and costs. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 67–80.
- Heinsohn, R. G. and Cockburn, A. (1994). Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proc. R. Soc. London B*, 256, 293–298.
- Jetz, W. and Rubenstein, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.*, 21, 72–78.
- Keller, L. and Reeve, H. K. (1994). Partitioning of reproduction in animal societies. *Trends Ecol. Evol.*, 9, 98–102.
- Kingma, S. A., Santema, P., Taborsky, M., and Komdeur, J. (2014). Group augmentation and the evolution of cooperation. *Trends Ecol. Evol.*, 29, 476–484.
- Koenig, W. D. (1981). Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *Am. Nat.*, 117, 421–443.
- Koenig, W. D. and Haydock, J. (2004). Incest and incest avoidance. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 142–156.
- Koenig, W. D. and Mumme, R. L. (1987). *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton, NJ: Princeton University Press.
- Koenig, W. D. and Pitelka, F. A. (1981). Ecological factors and kin selection in the evolution of cooperative breeding in birds. In: *Natural Selection and Social Behavior: Recent Research and New Theory*, ed. R. D. Alexander and D. W. Tinkle. Concord, MA: Chiron press, pp. 261–280.
- Koenig, W. D. and Walters, E. L. (2015). Temporal variability and cooperative breeding: testing the bet-hedging

- hypothesis in the acorn woodpecker. *Proc. R. Soc. London B*, 282, 20151742.
- Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L., and Stanback, M. T. (1992). The evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.*, 67, 111–150.
- Koenig, W. D., Van Vuren, D., and Hooge, P. N. (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.*, 12, 514–517.
- Koenig, W. D., Haydock, J., and Stanback, M. T. (1998). Reproductive roles in the cooperatively breeding acorn woodpecker: incest avoidance versus reproductive competition. *Am. Nat.*, 151, 243–255.
- Koenig, W. D., Walters, E. L., and Haydock, J. (2011). Variable helpers effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. *Am. Nat.*, 178, 145–158.
- Kokko, H. and Ekman, J. (2002). Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *Am. Nat.*, 160, 468–484.
- Kokko, H., Johnstone, R. A., and Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. London B*, 268, 187–196.
- Kramer, K. L. and Russell, A. F. (2014). Kin-selected cooperation without lifetime monogamy: human insights and animal implications. *Trends Ecol. Evol.*, 29, 600–606.
- Lukas, D. and Clutton-Brock, T. H. (2012). Cooperative breeding and monogamy in mammalian societies. *Proc. R. Soc. London B*, 279, 2151–2156.
- Magrath, R. D. (2001). Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: a model for cooperatively breeding birds? *J. Anim. Ecol.*, 70, 370–385.
- Magrath, R. D. and Whittingham, L. A. (1997). Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. *Behav. Ecol. Sociobiol.*, 41, 185–192.
- Magrath, R. D., Johnstone, R. A., and Heinsohn, R. G. (2004). Reproductive skew. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 157–176.
- Meade, J., Nam, K.-B., Beckerman, A. P., and Hatchwell, B. J. (2010). Consequences of “load-lightening” for future indirect fitness gains by helpers in a cooperatively breeding bird. *J. Anim. Ecol.*, 79, 529–537.
- Mulder, R. A. and Langmore, N. E. (1993). Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.*, 45, 830–833.
- Nonacs, P. and Hager, R. (2011). The past, present and future of reproductive skew theory and experiments. *Biol. Rev.*, 86, 271–298.
- Pruett-Jones, S. G. and Lewis, M. J. (1990). Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature*, 348, 541–542.
- Raihani, N. J., Thornton, A., and Bshary, R. (2012). Punishment and cooperation in nature. *Trends Ecol. Evol.*, 27, 288–295.
- Reeve, H. K., Westneat, D. F., Noon, W. A., Sherman, P. W., and Aquadro, C. F. (1990). DNA “fingerprinting” reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *Proc. Natl. Acad. Sci. (USA)*, 87, 2496–2500.
- Reyer, H.-U. (1980). Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim. Behav.*, 32, 1163–1178.
- Reyer, H.-U. (1990). Pied kingfishers: ecological causes and reproductive consequences of cooperative breeding. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*, ed. P. B. Stacey and W. D. Koenig. Cambridge: Cambridge University Press, pp. 527–557.
- Riehl, C. (2013). Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. London B*, 280, 20132245.
- Rowley, I. and Russell, E. (1990). Splendid fairy-wrens: demonstrating the importance of longevity. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*, ed. P. B. Stacey and W. D. Koenig. Cambridge: Cambridge University Press, pp. 2–30.
- Rowley, I., Russell, E., and Brooker, M. (1993). Inbreeding in birds. In: *The Natural History of Inbreeding and Outbreeding*, ed. N. W. Thornhill. Chicago, IL: University of Chicago Press, pp. 304–328.
- Royle, N. J., Russell, A. F., and Wilson, A. J. (2014). The evolution of flexible parenting. *Science*, 345, 776–781.
- Rubenstein, D. R. (2011). Spatiotemporal environmental variation, risk aversion and the evolution of cooperative breeding in birds. *Proc. Natl. Acad. Sci. (USA)*, 108, 10816–10822.
- Rubenstein, D. R. and Lovette, I. J. (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.*, 17, 1414–1419.
- Russell, A. F., Langmore, N. E., Cockburn, A., Astheimer, L. B., and Kilner, R. M. (2007). Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science*, 317, 941–944.
- Schoech, S. J., Reynolds, S. J., and Boughton, R. K. (2004). Endocrinology. In: *Ecology and Evolution of Cooperative Breeding in Birds*, ed. W. D. Koenig and J. L. Dickinson. Cambridge: Cambridge University Press, pp. 128–141.
- Shen, S.-F. and Reeve, H. K. (2010). Reproductive skew theory unified: the general bordered tug-of-war model. *J. Theor. Biol.*, 263, 1–12.
- Smith, J. N. M. (1990). Summary. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*, ed. P. B.

- Stacey and W. D. Koenig. Cambridge: Cambridge University Press, pp. 593–611.
- Stacey, P. B. and Koenig, W. D. (eds.) (1990). *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*. Cambridge: Cambridge University Press.
- Stacey, P. B. and Ligon, J. D. (1987). Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *Am. Nat.*, 130, 654–676.
- Stacey, P. B. and Ligon, J. D. (1991). The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *Am. Nat.*, 137, 831–846.
- Starrfelt, J. and Kokko, H. (2012). Bet-hedging – a triple trade-off between means, variances and correlations. *Biol. Rev.*, 87, 742–755.
- Stern, C. A. (2012). Cooperation and competition in kin associations. Ph.D. thesis, Cornell University, Ithaca, New York.
- Webster, M. S., Pruett-Jones, S., Westneat, D. F., and Arnold, S. J. (1995). Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution*, 49, 1147–1157.
- Whittingham, L. A., Dunn, P. O., and Magrath, R. D. (1997). Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren (*Sericornis frontalis*). *Behav. Ecol. Sociobiol.*, 40, 261–270.