Climate, cooperation and social evolution

Sheng-Feng Shen[a] **and Dustin R Rubenstein**[b], [a]Biodiversity Research Center, Academia Sinica, Taipei, Taiwan; [b]Columbia University, New York, NY, United States

This is an update of Sheng-Feng Shen, Dustin R. Rubenstein, Environmental Uncertainty and Social Behavior, Editor(s): Jae Chun Choe, Encyclopedia of Animal Behavior (Second Edition), Academic Press, 2019, Pages 807–815, ISBN 9780128132524, https://doi.org/10.1016/B978-0-12-809633-8.90144-4.

Abstract

Ecology plays a critical role in shaping social evolution. Here we explore how environmental factors influence cooperative breeding behavior, a complex form of social behavior that involves more than two individuals caring for young. Both harsh and benign environments can promote cooperative breeding, which constitutes a paradox of environmental condition and sociality. Using the dual benefits framework to distinguish between different types of grouping benefits – resource defense benefits derived from groups defending critical resources versus collective action benefits resulting from social cooperation among group members – can help resolve this paradox. Instead of simply focusing on the behavioral decisions of why individuals stay at home or why they help parents from only the offspring's perspective, the dual benefits framework considers the fitness consequences of cooperation from both the perspectives of current group members (insiders) and of potential joiners (outsiders). The different grouping benefits of resource defense and collective action profoundly affect insider-outsider conflict resolution, resulting in predictable differences in the per capita productivity, group size, kin structure, and stability of the social group. Ultimately, the dual benefits framework allows researchers to make testable predictions about how the environment influences social evolution, as well as explore the ecological and evolutionary consequences of sociality.

Keywords

Bet hedging; Conflict; Cooperation; Cooperative breeding; Ecological constraints; Environmental uncertainty; Fluctuating environments; Grouping; Insider-outsider conflict; Optimal group size; Social evolution; Sociality

Glossary

Cooperative breeding A form of social system in which more than two individuals care for young. In most cooperatively breeding systems, some mature offspring delay dispersal, remain in their natal social groups, and often "help" raise their parents' offspring (their siblings) from subsequent breeding attempts.
Hamilton's Rule The idea that a gene for altruism will spread only if $rB > C$, where r is the genetic relatedness between two individuals, B is the benefit (in terms of reproductive units) gained by the recipient of the altruistic act, and C is the cost (in terms of reproductive units lost) to the individual performing the altruistic act.
Inclusive fitness A total measure of an individual's contribution of genes to the next generation generated by both direct fitness (derived from reproduction) and indirect fitness (which depends on social interactions with relatives).
Kin selection A form of natural selection that favors the reproductive success of the relatives an organism helps, even at a cost to the organism's own fitness.
Sociality Cooperative group living.

Key points

- The paradox of environmental quality and sociality argues that cooperative breeding emerges in both harsh, unpredictable environments and stable, benign environments, suggesting multiple pathways to social evolution.
- The dual-benefit framework helps resolves this paradox by distinguishing between two types of grouping benefits:
  - *Resource defense benefits*, which are critical in stable environments where the defense of high-value territories is essential.
  - *Collective action benefits*, which are important in harsh or fluctuating environments where group cooperation enhances survival and reproduction.
- Environmental conditions determine not only whether animals cooperate, but also how they cooperate:
  - Stable environments tend to promote kin-based groups focused on resource defense.
  - Fluctuating environments tend to favor more flexible social structures that can include both kin and non-kin group members.
- Group formation depends on both insider and outsider perspectives:
  - Insiders (current group members) and outsiders (potential joiners) may have different interests when it comes to group membership.
  - Resolution of insider-outsider conflict depends on the nature of grouping benefits.
- Species that use collective action benefits in harsh environments show greater resilience to environmental change:
  - They maintain larger geographic ranges than non-cooperative species.
  - They reach higher abundances than non-cooperative species.
  - They may be better equipped to cope with future climate variability.
- Understanding these dynamics has important implications for:
  - Predicting species responses to climate change.
  - The conservation of social species.
  - The evolution of complex social systems.

Introduction

Social behavior, ranging from temporary gatherings for mating to complex cooperative societies in which individuals work together to raise young, occurs in species across the animal kingdom, ranging from slime molds to humans. Of particular interest are cooperatively breeding species in which multiple individuals help care for offspring that are not their own, a behavior that puzzled even Charles Darwin. Why would any animal sacrifice its own reproductive opportunities to help others? The answer lies in the complex interplay between ecology and evolution. Environmental conditions play a crucial role in determining whether animals choose to live and reproduce alone or in groups. Some species form cooperative groups in stable, resource-rich environments where vacant high-quality territories are scarce, while others group together in harsh, unpredictable environments. This apparent paradox of social behavior occurring under both extremes of environmental conditions has led researchers to investigate not only why individuals join groups, but also what benefits they derive from breeding cooperatively. Understanding these dynamics has become increasingly important as climate change alters the environmental conditions experienced by social species, potentially affecting their ability to persist in some of the earth's most extreme environments where they currently thrive.

Animals of nearly every species on earth interact socially during their lifetimes. These interactions can vary from simply coming together only to procreate in solitary species to the formation of long-term social bonds in group-living species. The term social behavior describes interactions between individuals, which can be either positive (cooperative) and negative (competitive). When both interacting individuals receive a fitness benefit (referred to as a mutual benefit) or when the recipient receives a fitness benefit but the donor pays a fitness cost (referred to as altruism), organisms are said to be cooperating. Cooperation occurs in numerous species, particularly in those in which individuals associate together for extended periods of time, such as in most group-living species. Indeed, cooperation forms the basis of sociality, which is perhaps best defined as cooperative group living (Rubenstein and Abbot, 2017b).

Sociality has been a topic of great interest among biologists since Charles Darwin wrote *On the Origin of Species* more than 150 years ago (Darwin, 1859). Darwin was puzzled by the self-sacrificial behavior and presence of sterile caste in ants, topics that continue to intrigue biologists to this day. We now know that sociality occurs not just in insects, but broadly across animals as diverse as crustaceans and primates (Rubenstein and Abbot, 2017b). What's more, social animals occur in virtually every ecosystem on Earth, ranging from tropical rainforests and savannas to freshwater lakes and marine coral reefs. Given the broad and varied geographic and taxonomic distributions of social organisms, biologists have long been interested in explaining why some species are social and other are not, why social species tend to occur in some places but not others, and what factors drive animal social evolution. This article will address these questions by focusing on the role of environmental factors in driving animal social behavior, particularly forms of cooperation and cooperative societies. As we will see, for nearly 50 years, behavioral biologists have recognized the critical role that the environment plays in the formation and maintenance of animal societies.

Here we will focus primarily on vertebrate species whose form of social behavior involves more than two individuals caring for young. In these "cooperatively breeding species," non-breeding helpers typically forgo their own reproduction to help raise others' offspring. To understand why individuals would help raise offspring that are not their own, we must first recognize that genes are capable of not only being passed on directly via the production of offspring, but also indirectly through a relative's offspring (Hamilton, 1964). Indeed, kin selection – a form of natural selection that favors the reproductive success of the relatives an organism helps, even at a cost to the organism's own fitness – and inclusive fitness theory more generally (i.e., the idea that both direct and indirect benefits can influence fitness) has long been known as one mechanism that can promote the evolution of cooperative behavior and sociality, including in cooperatively breeding species (Hamilton, 1964). William D. Hamilton recognized that altruistic traits such as helping behavior in cooperatively breeding societies would become more common only if the indirect fitness gained by the altruist is greater than the direct fitness it loses as a result of its self-sacrificing behavior (Hamilton, 1964). Hamilton formalized this idea in what has become known as "Hamilton's Rule," the idea that a gene for altruism will spread only if $rB > C$, where r is the genetic relatedness between two individuals, B is the benefit (in terms of reproductive units) gained by the recipient of the altruistic act, and C is the cost (in terms of reproductive units lost) to the individual performing the altruistic act. Although relatedness is critical to Hamilton's Rule, the benefit B and cost C (which is generally considered in terms of environmental constraints on independent reproduction) terms, are just as important. When the inclusive fitness of solitary and social strategies are considered, we find that grouping benefits – generated when group productivity is greater than the sum of the expected direct fitness of individual group members if each were to breed on its own – are a necessary condition for group formation and stability (Shen et al., 2017; Keller and Reeve, 1994).

Sociality: Ecology and delayed dispersal

The early development of cooperative breeding theory was largely influenced by studies of "helper-at-the-nest" types of avian cooperatively breeding systems in which mature offspring delay dispersal, remain in their natal social groups, and often help to raise their parents' offspring (their siblings) from subsequent breeding attempts (Koenig and Mumme, 1987). In other words, the emphasis by most researchers of vertebrate social evolution has long been on the formation of family groups. As a consequence, early studies of cooperative breeding behavior in birds mainly focused on answering two questions: (1) Why do some individuals within a group delay dispersal?; and (2) Why do some individuals within a group "help"? (Brown, 1987; Emlen, 1984, 1991; Dickinson and Hatchwell, 2004).

Many of the earliest studies on avian cooperative breeding occurred in the tropics where environments are relatively stable and population densities are high. The "habitat saturation hypothesis" was developed to resolve the first question, namely why mature offspring forgo current reproduction and stay at home when the alternative of breeding solitarily yields greater fitness (i.e., solitary breeders usually have the highest per capita productivity) (Selander, 1964). The key insight of the habitat saturation hypothesis was that current breeding options for mature offspring can be severely limited because high population density leads to habitat saturation, which can in turn lead to a shortage of acceptable territorial vacancies for solitary breeders. Under such circumstances, individuals that temporarily delay dispersal and remain in their natal social groups until suitable solitary breeding vacancies become available can realize greater lifetime fitness than individuals that disperse prematurely (Brown, 1974, 1987; Emlen, 1982, 1984; Koenig, 1981; Koenig and Pitelka, 1981; Koenig et al., 1992).

The habitat saturation hypothesis was subsequently expanded into the "ecological constraints hypothesis" (Emlen, 1982, 1984) to include situations where current breeding options are limited because of either (1) a lack of breeding openings in stable environments or (2) the high cost of rearing young in fluctuating environments. Most empirical tests of the ecological constraints hypothesis have focused on the idea that habitat saturation promotes delayed dispersal and the evolution of helping behavior (Koenig and Mumme, 1987). However, this second constraint related to the costs of rearing young in fluctuating environments is not caused by a shortage of breeding vacancies or mates, but rather by a limit on the ability of solitary pairs to successfully reproduce without helpers in low quality years. Emlen considered "the erratic changes in rainfall in unpredictable environments as creating the functional equivalents of breeding openings and closures" (Emlen, 1982, page 37). Only much later did researchers begin to explore the role of environmental variation in driving helping behavior and the evolution of cooperative breeding (Lukas and Clutton-Brock, 2017; Griesser et al., 2017; Jetz and Rubenstein, 2011; Rubenstein and Lovette, 2007; Rubenstein, 2011). Thus, the ecological constraints hypothesis focused largely on the role of spatial environmental variation and ecological constraints in driving delayed dispersal and helping behavior, though it also considered how temporal variation influences these processes.

Although both of these early hypotheses emphasized how ecological constraints on independent breeding could promote cooperation, the "benefits of philopatry hypothesis" was later proposed to emphasize the unique benefits found only on the natal territory, which can increase an offspring's survival, reproduction, or future breeding opportunities, and, thus, may also drive delayed dispersal (Stacey and Ligon, 1987, 1991). The benefits of philopatry and ecological constraints hypotheses are now often considered to be "two sides of the same coin" because both compare the fitness consequences of the same decision of joining versus dispersing from one's natal social group (Emlen, 1994; Koenig et al., 1992; Mumme, 1997). In other words, they represent the two key parameters – B and C – in Hamilton's Rule. One key difference between them, however, is that the ecological constraints hypothesis focuses on mean fitness values related to helping behavior, whereas the benefits of philopatry hypothesis focuses on variance in fitness (Rubenstein, 2011), a topic we shall return to later.

The dual benefits framework

The ecological constraints and benefits of philopatry hypotheses have been used to explain the formation of family groups in a variety of vertebrate species ranging from birds to mammals to fish, yet many authors have questioned the predictive power of these hypotheses because numerous species seemingly face equally strong ecological constraints but do not exhibit delayed dispersal nor breed cooperatively (Smith, 1990; Covas and Griesser, 2007; Hatchwell and Komdeur, 2000; Kokko, 2007; Brockmann, 1997; Koenig et al., 1992; Kokko and Lundberg, 2001). Moreover, theoretical models have also challenged the assumption that ecological constraints are a necessary condition for the evolution of either offspring delayed dispersal or cooperative breeding (Pen and Weissing, 2000; Kokko and Lundberg, 2001).

One problem with the ecological constraints and benefit of philopatry hypotheses is that they largely focus on offspring decisions to remain in the natal group. However, social group formation is not just based on the decisions of offspring; parents also have a say in whether they will allow their offspring to remain on the natal territory. More generally, unrelated immigrants – "outsiders" – can also try to join a social group and the current group members – "insiders" – will try to accept or repel a potential joiner based on their own interests (Giraldeau and Caraco, 1993, 2000; Higashi and Yamamura, 1993). Conflict between insiders and outsiders (referred to as insider-outsider conflict) often exists because the fitness interests over group membership might not be the same for the two parties. Interestingly, when the interests of both insiders and outsiders are considered, the necessary – but not sufficient – condition for group formation is that there must be grouping benefits, such that the total group productivity must be greater than the sum of the expected fitnesses of each group member if each individual were to breed on their own, taking into account changes in long-term genetic contributions due to fluctuating environments (Shen et al., 2017). Two main types of grouping benefits have been proposed under the dual benefits framework: resource defense and collective action benefits (Shen et al., 2017). Importantly, these different grouping benefits profoundly affect the per capita productivity, group size, kinship composition, and stability of the resulting social groups, a topic we explore in greater detail below.

Resource defense benefits

An individual will only benefit by joining a cooperatively breeding group if such membership provides fitness advantages over living as a solitary breeder or as part of a breeding pair. Most organisms require critical resources from the environment (e.g., an abundance of food, shelter, safe breeding sites, etc.) for successful reproduction. When such resources are distributed heterogeneously in space, they become economically defendable (Emlen and Oring, 1977; Brown, 1964). Resource defense (RD) benefits refer to one category of such benefits not available to outsiders and that are obtained from access to, and familiarity with, the ecological resources controlled by the group. RD benefits can enhance the survival of group members when the quality of the habitat (or other resources) controlled by the group is superior to that in surrounding areas. Access to (and familiarity with) high quality food resources and safe habitat can reduce the risks of starvation and predation, respectively (Ekman et al., 2004). RD benefits also include reproductive advantages resulting from increased (current and future) access to potential mates and increased (future) access to high quality breeding opportunities. Examples include using the group's defended area as a "safe haven" from which to prospect for mates or nearby breeding vacancies (Zack, 1990; Kokko and Ekman, 2002), budding off a portion of the group's defended area for personal reproduction (Woolfenden and Fitzpatrick, 1984), or inheriting the resources of the group by becoming its dominant breeder (Stacey and Koenig, 1990).

The RD benefit concept assumes that group-controlled resources are important for survival and reproduction. This is most likely to be true when population density is high (leading to habitat saturation) and critical resources are spatially and temporally distributed so as to be defensible by groups. When such conditions apply, the intensity of competition to occupy territories of high resource quality is heightened, increasing the likelihood that an outsider (an individual or pair not in a group) will benefit from group membership and breeding cooperatively. The RD benefit concept also assumes that resources are *fixed* in the sense that the activities of group members do not significantly increase the quality or quantity of resources accessible to the group.

Collective action benefits

We define a collective action (CA) benefit as any grouping benefit resulting from social cooperation among group members (Shen et al., 2017). Such cooperation is generated by active social coordination between group members and may produce benefits that increase reproductive success (e.g., if larger groups better provision or protect dependent young), decrease predation risk (e.g., by alarm calling, group mobbing or attacking predators), enhance foraging efficiency (e.g., by information sharing, social storing of food or cooperative hunting), or reduce energy expenditure (e.g., by social huddling to conserve energy) (Whitehouse and Lubin, 2005; Krause and Ruxton, 2002). We exclude benefits arising from passive dilution of simply being in an aggregation (i.e., selfish herd effects).

The paradox of environmental quality and sociality

Over the past decade, an accumulation of evidence has shown that social species are distributed widely in both stable, benign environments as well as in harsh, fluctuating environments. For example, cooperatively breeding starlings tend to inhabit fluctuating environments with highly variable rainfall (Rubenstein and Lovette, 2007), but cooperatively breeding hornbills predominantly live in temporally stable areas (Gonzalez et al., 2013). Cooperatively breeding cichlid fishes are more likely than non-social ones to be distributed in temporally and spatially stable environments (Dey et al., 2017). And finally, cooperatively breeding birds (Jetz and Rubenstein, 2011) and mammals (Lukas and Clutton-Brock, 2017)—including humans (Martin et al., 2020)—occur more frequently in temporally fluctuating environments than the non-cooperative species. These contrasting patterns of environmental quality and sociality constitute a puzzle that has become known as the paradox of environmental quality and sociality (Lin et al., 2023; Liu et al., 2020; Shen et al., 2017).

One conceptual obstacle to understanding the evolution of cooperative breeding is determining why both benign and harsh environments lead to cooperative behavior, a phenomenon that constitutes "the paradox of environmental quality and sociality." Experienced researchers of cooperative breeding might quickly argue that the ecological constraints hypothesis actually resolved this paradox long ago. That is, cooperative breeding groups form because current breeding options are limited for mature offspring in both benign and harsh environments. However, as many researchers have pointed out, adopting an overly general definition of ecological constraints makes it difficult to obtain useful, testable predictions and can lead to facile post hoc identification of constraints (Hatchwell and Komdeur, 2000; Kokko and Ekman, 2002). Evidently, the adaptive significance of cooperative breeding in many social species remains elusive (Wcislo and Tierney, 2009; Silk, 2007; Cockburn and Russell, 2011). How then can we solve the paradox of environmental quality and sociality with empirical studies of cooperatively breeding vertebrates?

Dual benefits and the paradox of environmental quality and sociality

The dual benefits framework can help solve the paradox of environmental quality and sociality because it requires distinguishing between different types of grouping benefits that might underly why cooperatively breeding groups form. In particular, this framework allows for clear manipulative experiments with testable predictions about group stability, kinship composition, and insider-outsider conflict during the group formation process in order to understand the evolution of sociality at both intra- and interspecific levels. Although an increasing number of comparative studies have attempted to identify key social and ecological factors promoting sociality (Cornwallis et al., 2017; Rubenstein and Abbot, 2017a; Lukas and Clutton-Brock, 2017; Griesser et al., 2017), recent empirical evidence has begun to help clarify how these different benefits emerge. For example, studies of burying beetles demonstrate that climate (temperature) and competition (both intra- and interspecific) independently and synergistically influence sociality through different grouping benefits that vary along environmental gradients (Liu et al., 2020). At low elevations where interspecific competition is intense, groups gain from the collective action benefit of increased competitive ability. In contrast, pairs have higher fitness at intermediate elevations where intraspecific competition is greatest because resource defense is the key grouping benefit. Furthermore, theoretical modeling and phylogenetic comparative analyses across birds have shown that these different grouping benefits have distinct ecological consequences, with species that cooperate in harsh or fluctuating environments achieving larger ranges and greater abundances than non-cooperative species (Lin et al., 2023).

Although understanding which types of benefit individuals receive from grouping is essential for determining why animals form groups and for resolving the paradox of environmental quality and sociality, doing so can be challenging. When the type of potential grouping benefit an individual can receive by joining a cooperative group is a form of direct benefit (versus only an indirect benefit from raising relatives), it is critical to determine whether it is of the RD or CA type. When both categories of benefits may apply, the best way to empirically determine which type of benefit is primary for any given system is to conduct separate experiments manipulating each type of benefit (Shen et al., 2017). Specifically, manipulations of critical resources controlled by cooperatively breeding groups should cause predictable changes in group size if access to resources is an important RD benefit of cooperatively breeding group membership. Conversely, manipulations that reduce the efficiency of, or need for, coordinated social cooperation among cooperatively breeding group members should cause predictable changes in the productivity or size of the social group if enhanced social cooperation is an important CA benefit maintaining cooperatively breeding groups. In Table 1, we describe six experimental manipulations presented originally by Shen et al. (2017), as well as the expected results if the system is primarily one of RD, or CA, benefits.

The ecological constraints hypothesis versus the dual-benefits framework

The dual benefits framework differs from the ecological constraints hypothesis in two major ways: (1) both the insider's and outsider's perspectives are considered in the dual benefits framework, whereas only the insider's perspective is considered in the ecological constraints hypothesis; and (2) two different types of grouping benefits are clearly distinguished in the dual benefits framework but not the ecological constraints hypothesis, which has profound implications for group formation and on kinship structure. Considering insider-outsider conflict also helps us to understand diverse strategies regarding group formation and stability in a unified framework. For example, a joining outsider can work harder to provide some CA benefits to compensate the direct fitness loss of sharing resources, as proposed by "pay-to-stay" models for the evolution of cooperative breeding (Bergmler et al., 2005; Kokko et al., 2002; Gaston, 1978). Importantly, instead of only considering an offspring's dispersal decision, insider-outsider conflict theory is incorporated into the dual benefits framework to help identify which party's interests are more important in affecting group formation under different RD and CA benefit scenarios.

Table 1 Summary of critical experiments testing the relative importance of resource defense benefits versus collective action benefits in the formation and maintenance of cooperatively breeding groups.

Grouping benefit	*Critical experiment*	*Predicted results*	*Species*	*References*
Resource defense	Create available high quality resource outside the control of existing cooperative social groups.	Individuals disperse and defend the newly available resources.	Seychelles warblers	Komdeur (1992)
			Superb fairy wrens	Pruett-Jones and Lewis (1990)
			Red cockaded woodpeckers	Walters et al. (1992)
			Cichlid fishes (*N. pulcher*)	Heg et al. (2008)
			Hover wasps	Field et al. (1998)
	Increase critical resource within the control of existing cooperative social groups.	Larger proportion of young delay dispersal	Carrion crows	Baglione et al. (2006)
	Reduce critical resource within the control of existing cooperative social groups.	Smaller proportion of young delay dispersal	Western bluebirds	Dickinson and McGowan (2005)
Collective action	Increase the importance of collective action benefit by manipulating critical ecological environment.	Larger proportion of young delay dispersal	White fronted bee-eaters	Emlen (1982), Emlen (1990), Emlen and Wrege (1991)
			Pied kingfishers	Reyer (1990)
	Decrease the importance of collective action benefit by manipulating critical ecological environment.	Smaller proportion of young delay dispersal	Sociable weavers	Covas et al. (2004)
			Cichlid fishes (*N. pulcher*)	Heg et al. (2004)
	Manipulate group size and/or composition.	Effects depend on magnitude of the collective action benefit	gray-crowned babblers	Brown et al. (1982)
			Siberian jays	Ekman and Griesser (2002)
			Cichlid fishes (*N. pulcher*)	Heg et al. (2004)
			Hover wasps	Field et al. (2000)

Determining the relative importance of the two types of benefits requires conducting separate experiments manipulating each type of benefit in the same species.
After Shen S-F, Emlen ST, Koenig WD, and Rubenstein DR (2017) The ecology of cooperative breeding behaviour. *Ecology Letters* 20: 708–720.

Although other hypotheses to explain the evolution of cooperative breeding behavior considered different types of benefits, they were largely confounded by a lack of clarity. For example, the benefits of philopatry hypothesis included both "access to critical resources" and "group benefits" as benefits of remaining only in the natal group (Stacey and Ligon, 1987, 1991). Similarly, the ecological constraints hypothesis included what amount to RD benefits (in stable environments) and CA benefits (in harsh years in fluctuating environments) as benefits of living in cooperatively breeding groups (Emlen, 1982). Thus, the grouping benefit types were confounded in each of the original hypotheses, which therefore lacked power for generating critical predictions for distinguishing between them. In contrast, distinguishing RD from CA benefits under the dual benefits framework allows these concepts to be reconfigured into clear and testable alternative hypotheses and predictions.

Finally, kin selection has a central role in the dual benefits framework. By employing Hamilton's inclusive fitness theory, we can show that if the primary grouping benefit is of the RD type, the direct fitness of current group members decrease when an outsider is accepted into the group (Shen et al., 2017). Thus, only related outsiders will be accepted to join the group when they have a low probability of finding a breeding vacancy (high habitat saturation, Fig. 1(a-b)). Therefore, determining "why offspring remain the group" is not the appropriate question to ask to understand group formation in this case; instead, researchers should determine "why insiders accept potential joiners," a topic that depends greatly on the relatedness among insiders and outsiders (Fig. 1). Furthermore, the direct fitness cost can be too high for insiders (e.g., parents) to accept related potential joiners, which may outweigh the indirect fitness gain of providing a "safe haven" or sharing resources to joining relatives (Fig. 1(a-b)). Thus, the dual benefits framework explains why habitat saturation occurs commonly but does not always lead to offspring delaying dispersal in all species.

When the primary type of grouping benefit is of the CA type and an outsider can substantially increase the direct fitness of current group members, then the insiders should accept the potential joiner (Fig. 1(c-d)). In this scenario, an outsider's decision to join the group and help or disperse will be the key to determining if social groups forms (Reeve, 1998). Nevertheless, even in this CA benefit case, the degree of relatedness and of habitat saturation – represented by the probability of finding a breeding vacancy – will still influence the joining decision of a potential joiner: an outsider that is either related or unrelated to the insiders will be more likely to join the group and help when the degree of habitat saturation is high (Fig. 1(c-d)). This scenario not only explains kin group formation, but also why non-kin groups form in many species.

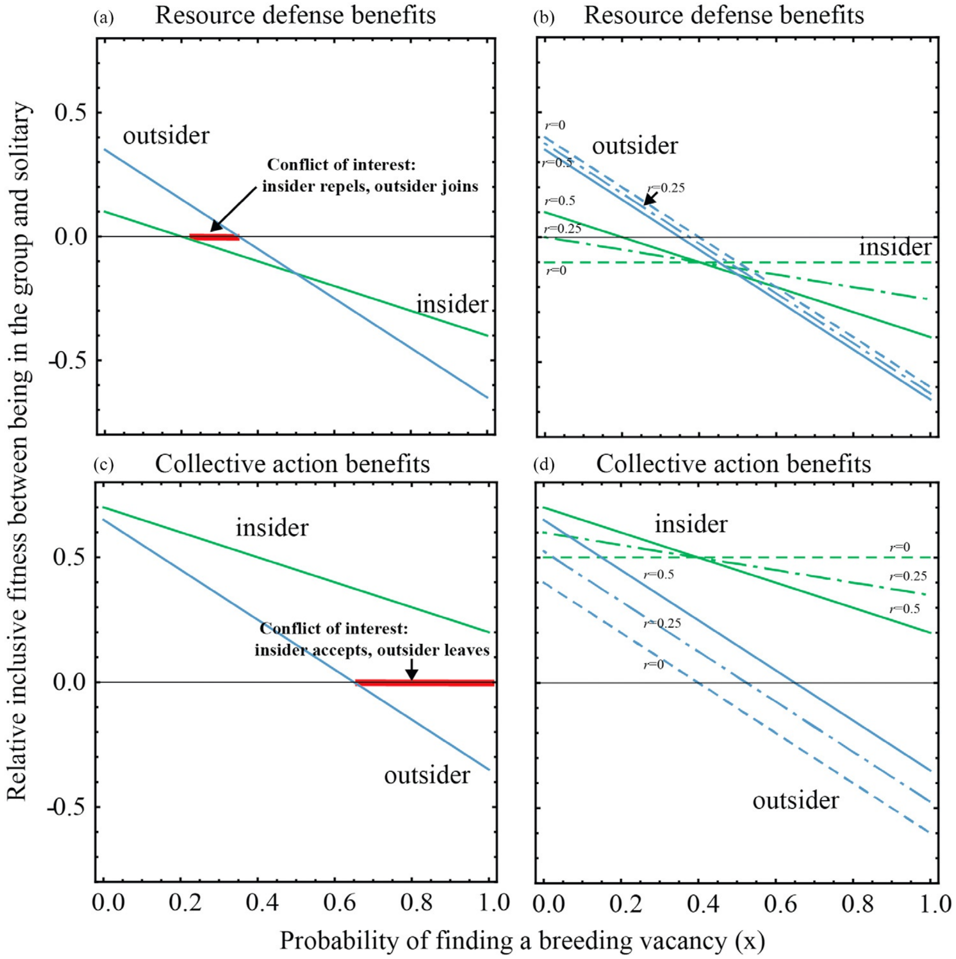

Fig. 1 The relationship between relative inclusive fitness of being in the group versus being solitary for an outsider (blue line, from inequality A1), and of an insider accepting versus rejecting the outsider (green line, from inequality A2). In some cases, a joining outsider *decreases* the direct fitness of the insider ($Gi = 0.9$, $L = 1$, $r = 0.5$, $Go = 0.4$), representing a scenario of resource defense benefits (a) when genetic relatedness between insiders and an outsider is 0.5, and (b) when relatedness varies. In other cases, a joining outsider *increases* the direct fitness of the insider ($Gi = 1.5$, $L = 1$, $Go = 0.4$), representing a scenario of collective action benefits (c) when genetic relatedness between insiders and an outsider is 0.5, and (d) when relatedness varies. Red lines represent the regions where conflicts of interest over group formation exist between the insider and outsider. After Shen S-F, Emlen ST, Koenig WD, and Rubenstein DR (2017) The ecology of cooperative breeding behaviour. *Ecology Letters* 20: 708–720.

Dual benefits and environmental quality

The dual benefits framework has proven useful for understanding social evolution in both stable and variable environments. However, to fully grasp how environmental conditions shape social behavior, we must carefully consider how temporal environmental variation influences both the ecological and social conditions that cooperative breeders experience. Environmental fluctuations can substantially impact not only the immediate costs and benefits of social living, but also the long-term evolutionary trajectories of social species. To understand these complex relationships between environmental variation and sociality, we need to examine how natural selection operates differently in fluctuating versus stable environments.

The dual benefits framework suggests that delayed dispersal is not the reason that all cooperatively breeding groups form. As the ecological constrains hypothesis originally argued, environmental fluctuation might also influence sociality. Indeed, environmental fluctuations can have substantial impacts on both the environmental and the social conditions (e.g., population size) that cooperative breeders experience. How environmental quality – the harshness or benignness of environmental conditions – influences the evolution of sociality can be understood by assessing the different grouping benefits associated with varying environmental conditions, as we described previously. However, since environmental conditions can also influence population size and the relative fitness of a genotype or a phenotype, the way that natural selection operates in fluctuating environments is different than the way it does in stable environments. Specifically, the geometric mean of fitness, which can be approximated by the arithmetic mean fitness, w, and the variance in fitness, σ^2, through time, approximately equals $G \approx w - \sigma^2/2w$ (Tuljapurkar, 1982; Gillespie, 1977, 1991; Orr, 2009). Based on this approximation, a cooperative breeding strategy can be selected for either if it has a higher arithmetic mean fitness or a smaller arithmetic mean but a lower variance in fitness than a solitary strategy. It is also clear that arithmetic mean fitness is simply a special case of the geometric mean of fitness when the variance of fitness equals to zero. We therefore apply the concept of geometric mean fitness to the evolution of cooperative breeding behavior in both stable environments and fluctuating environments in the following sections to illustrate why cooperative breeding behavior can evolve for different reasons in different types of environments.

Dual benefits in temporally stable environments

By definition, ecological and social conditions that lead to defendable resources are critical for understanding the evolution of RD benefits in social groups. Stable but patchy environments are not only more likely to lead to RD benefits, but also to high population density, which intensifies intraspecific competition for critical resources (i.e., high degree of habitat saturation), making defending group resources more valuable. Indeed, much empirical evidence has demonstrated that stable environments and high population densities favor cooperatively breeding behavior, including the classic study in Seychelles warblers (*Acrocephalus sechellensis*) that showed birds only began exhibiting helping behavior when the population size grew so large that not all individuals were able to occupy their own territory and breed. Similarly, RD benefits explain why carrion crows (*Corvus corone*) exhibit helping behavior in Spain where the population density is low and territories are defensible year-round, but not in central Europe where the population density is high (Baglione et al., 2005). That is, in the Spanish population where habitat is spatially heterogeneous, offspring born on high quality territories benefit by remaining on their natal territory to enjoy the RD benefits of higher survival or territorial inheritance, even when population density is low (Koenig et al., 1992; Komdeur, 1992).

Although RD benefits are likely to be the most important reason for group formation in stable environments, there are empirical examples – particularly in obligate cooperatively breeding species – where CA benefits can also be important for the evolution of cooperative breeding in stable environments. For example, increased provisioning efficiency is the primary CA benefit in cooperatively breeding pied kingfishers (*Ceryle rudis*) living in two spatially distinct Rift Valley lakes. In these lakes, food availability differs primarily due to stable environmental characteristics such as water turbidity, distance to fishing grounds, and prey energy content: Lake Victoria presenting consistently more challenging fishing conditions than Lake Naivasha (Reyer and Westerterp, 1985; Reyer, 1990). Indeed, the positive fitness effect of helpers was greater at Lake Victoria than Lake Naivasha because the primary prey fishes are more difficult to catch and nutritionally poorer in Lake Victoria (see Shen et al., 2017).

Dual benefits in temporally fluctuating environments

There are three non-mutually exclusive hypotheses concerning the evolution of cooperative breeding in harsh and fluctuating environments, all of which generally emphasize CA benefits in poor conditions. The "hard life hypothesis" argues that individuals maintain stable groups through different environmental conditions, but that CA benefits such as cooperative provisioning of young are greater in hard times (Koenig and Mumme, 1987; Koenig et al., 2011). Recent theoretical work shows that low quality mean environmental conditions and high environmental fluctuations can have similar effects on the evolution of cooperative behavior, as environments with greater fluctuations include periods of both low and high environmental quality, leading to stronger selection for social group formation during harsh periods with small population sizes than during benign periods (Lin et al., 2023). Thus, if cooperation becomes essential for reproduction in low quality years, we expect that both total and per capita productivity will be higher in groups than in pairs, as demonstrated in burying beetles where groups gain collective action benefits through increased competitive ability against interspecific competitors under poor conditions (Liu et al., 2020).

In contrast, the "fission-fusion hypothesis" proposes that individuals adjust their breeding group size to current environmental conditions – forming larger groups in low quality years to obtain CA benefits in poor conditions but becoming solitary or forming smaller groups in good conditions (Rubenstein and Lovette, 2007; Emlen, 1982). In this case, since group size is flexibly adjusted to environmental conditions and grouping benefits, cooperative breeding should lead to lower fitness variance and higher mean fitness. However, whether the conflict of interest between insiders and outsiders exists and, if it does, how these individuals resolve such conflict to achieve such flexible social structure remains to be addressed. Finally, the "bet-hedging hypothesis" argues that unpredictability in highly variable environments favors cooperative breeding as a strategy to reduce interannual variance in the reproductive success of social groups, a CA type benefit (e.g., Rubenstein and Lovette, 2007; Jetz and Rubenstein, 2011). Although there have been a handful of empirical tests of these ideas (Capilla-Lasheras et al., 2021; Kerr et al., 2024; Koenig and Walters, 2015; Rubenstein, 2011; Nelson-Flower et al., 2018), recent theoretical and comparative evidence suggests that species using CA benefits in harsh or fluctuating environments may be more resilient to environmental change than both non-social species and those using resource defense benefits in benign environments (Lin et al., 2023). This greater resilience is reflected in larger geographic ranges and higher abundances among cooperative breeders occurring in harsh and fluctuating environments compared to non-cooperative species (Lin et al., 2023).

Finally, these alternative hypotheses are often summarized as emphasizing the relative importance of environmentally-driven mean fitness versus variance in fitness for cooperative breeders (Rubenstein, 2011). Recent empirical studies have shown that climate (temperature) and competition (both intra- and interspecific) independently and synergistically influence which type of cooperative benefit emerges (Liu et al., 2020). Although most theories regarding the evolution of cooperative breeding dating back to the ecological constraints hypothesis have largely focused on offspring delayed dispersal decisions (i.e., from the outsider's perspective), these three hypotheses have implicitly considered the fitness benefit from the breeders,' or the insiders' perspectives.

Why an outsider prefers to join a cooperatively breeding group in a fluctuating environment remains to be explored using insider-outsider conflict theory, but empirical evidence suggests there can be reproductive and survival advantages from doing so (Guindre-Parker and Rubenstein, 2020; Shah and Rubenstein, 2023). Moreover, when the interests of both insiders and outsiders are considered simultaneously for species experiencing fluctuating environments, the primary grouping benefits for each player remains unclear. Thus, there remains much work to be done examining the grouping benefits of cooperative breeders – both group members and potential joiners – that experience fluctuating environmental conditions.

Ecology and sociality: A look forward

For more than 50 years, behavioral biologists have recognized the role that ecological and environmental factors play in shaping social behavior in vertebrates and other animals. However, the historical emphasis on ecological constraints to dispersal and independent breeding largely failed to consider the many types of benefits that animals receive by forming groups, as well as the role that temporal environmental variation plays in social evolution. More recently, the dual benefits framework has provided a way to make testable predictions for why animal social behavior has evolved, and it has done so in a way that explicitly considers both group members and potential joiners, and species that live in both harsh and unpredictable environments as well as those in stable and benign environments. Recent empirical studies have provided strong support for this framework, showing how different types of cooperative benefits emerge under different environmental conditions (Liu et al., 2020) and generate distinct ecological consequences (Lin et al., 2023).

Ultimately, the dual benefits framework emphasizes the grouping benefits that individuals receive by breeding cooperatively. Such an integrative understanding of grouping benefits at both intra- and interspecific levels helps explain why particular species breed cooperatively, and also reveals broader ecological patterns. For example, theoretical modeling and comparative analyses have shown that species forming groups for CA benefits in harsh and fluctuating environments tend to have larger ranges and greater abundances than non-cooperative species, while those forming groups for RD benefits in stable and benign environments do not show such patterns (Lin et al., 2019, 2023). These findings help resolve long-standing questions about the ecological consequences (e.g., host and species distributional ranges) and evolutionary consequences (e.g., diversification rates in social and non-social lineages) of sociality in both RD and CA benefit species (Brooks et al., 2017; Sun et al., 2014; Wilson, 1990, 2012).

Understanding how environmental fluctuations shape social evolution has become increasingly important in the context of global climate change. Research examining the relationship between cooperative breeding and environmental conditions suggests that social strategies may play a critical role in determining species' responses to environmental challenges. Comparative analyses and theoretical models indicate that social species that adopt cooperative strategies in fluctuating and harsh environments exhibit greater population resilience than solitary species or those that cooperate primarily under stable conditions (Lin et al., 2023). By examining both historical patterns and current fitness benefits of grouping, researchers can better predict how different forms of social organization may influence species' abilities to cope with increasing environmental fluctuations. This integrative approach provides valuable insights for predicting how social species may respond to future environmental change.

Conclusion

The relationship between environmental conditions and social evolution has turned out to be more complex than originally theorized. Through the dual-benefit framework, we can now better understand why cooperative breeding occurs in both harsh and benign environments, which was once thought to be a paradox. Resource defense benefits explain social behavior in stable, high-quality environments where the defense of critical resources is paramount, while collective action benefits drive cooperation in harsh or fluctuating environments where group members must work together to survive and reproduce. This framework has provided not only theoretical insights, but also practical predictions that have been supported by empirical evidence across species. Recent studies have shown that species that form groups for the benefits of collective action in harsh environments tend to be more resilient to environmental change, maintaining larger geographic ranges and higher abundances than their non-cooperative counterparts. As our planet faces increasing environmental fluctuations due to climate change, understanding these dynamics is critical. The dual-benefit framework suggests that some social species, particularly those that have adapted to harsh or variable conditions through the benefits of collective action, may be better equipped to face future environmental challenges. However, species that evolved cooperative breeding primarily for resource defense in stable environments may be more vulnerable to environmental change. This understanding not only advances our knowledge of social evolution, but also provides valuable insights for predicting and potentially protecting social species in an increasingly unstable world.

References

Baglione V, Marcos JM, Canestrari D, et al. (2005) Does year-round territoriality rather than habitat saturation explain delayed natal dispersal and cooperative breeding in the carrion crow? *The Journal of Animal Ecology* 74: 842–851.

Baglione V, Canestrari D, Marcos JM, and Ekman J (2006) Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 273: 1529–1535.

Bergmler R, Heg D, and Taborsky M (2005) Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 272: 325–331.

Brockmann HJ (1997) Cooperative breeding in wasps and vertebrates: The role of ecological constraints. In: Choe JC and Crespi BJ (eds.) *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge: Cambridge University Press.

Brooks KC, Maia R, Duffy JE, Hultgren KM, and Rubenstein DR (2017) Ecological generalism facilitates the evolution of sociality in snapping shrimps. *Ecology Letters* 20: 1516–1525.

Brown JL (1964) The evolution of diversity in avian territorial systems. *The Wilson Bulletin* 76: 160–169.

Brown JL (1974) Alternate routes to sociality in jays-with a theory for the evolution of altruism and communal breeding. *American Zoologist* 14: 63–80.

Brown JL (1987) *Helping and Communal Breeding in Birds*. Princeton: Princeton University Press.

Brown JL, Brown ER, Brown SD, and Dow DD (1982) Helpers: Effects of experimental removal on reproductive success. *Science* 215: 421–422.

Capilla-Lasheras P, Harrison X, Wood EM, Wilson AJ, and Young AJ (2021) Altruistic bet-hedging and the evolution of cooperation in a Kalahari bird. *Science Advances* 7: eabe8980.

Cockburn A and Russell AF (2011) Cooperative breeding: A question of climate? *Current Biology* 21: R195–R197.

Cornwallis CK, Botero CA, Rubenstein DR, et al. (2017) Cooperation facilitates the colonization of harsh environments. *Nature Ecology & Evolution* 1.

Covas R and Griesser M (2007) Life history and the evolution of family living in birds. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 274: 1349–1357.

Covas R, Doutrelant C, and du Plessis MA (2004) Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 271: 827–832.

Darwin C (1859) *On the Origin of Species by Means of Natural Selection*. London: Murray.

Dey CJ, O'connor CM, Wilkinson H, et al. (2017) Direct benefits and evolutionary transitions to complex societies. *Nature Ecology & Evolution* 1.

Dickinson JL and Hatchwell BJ (2004) Fitness consequences of helping. In: Koenig WD and Dickinson JL (eds.) *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge: Cambridge University Press.

Dickinson JL and McGowan A (2005) Winter resource wealth drive's delayed dispersal and family-group living in western bluebirds. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 272: 2423–2428.

Ekman J and Griesser M (2002) Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 269: 1709–1714.

Ekman JAN, Dickinson JL, Hatchwell B, and Griesser M (2004) Delayed dispersal. In: Koenig WD and Dickinson JL (eds.) *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge: Cambridge University Press.

Emlen ST (1982) The evolution of helping I. An ecological constraints model. *The American Naturalist* 119: 29–39.

Emlen ST (1984) Cooperative breeding in birds and mammals. In: Krebs JR and Davies NB (eds.) *Behavioural Ecology: An Evolutionary Approach*, 2nd edn. Oxford: Blackwell Science.

Emlen ST (1990) White-fronted bee-eaters: Helping in a colonially nesting species. In: Stacey PB and Koenig WD (eds.) *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*, pp. 487–526. Cambridge: Cambridge University Press.

Emlen ST (1991) Evolution of cooperative breeding in birds and mammals. In: Krebs JR and Davies NB (eds.) *Behavioural Ecology: An Evolutionary Approach*, 3rd edn. Oxford: Blackwell Science.

Emlen ST (1994) Benefits, constraints and the evolution of the family. *Trends in Ecology & Evolution* 9: 282–284.

Emlen ST and Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223.

Emlen ST and Wrege PH (1991) Breeding biology of white-fronted bee- eaters at Nakuru: The influence of helpers on breeder fitness. *The Journal of Animal Ecology* 60: 309–326.

Field J, Foster W, Shreeves G, and Sumner S (1998) Ecological constraints on independent nesting in facultatively eusocial hover wasps. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 265: 973–977.

Field J, Shreeves G, Sumner S, and Casiraghi M (2000) Insurance-based advantage to helpers in a tropical hover wasp. *Nature* 404: 869–871.

Gaston AJ (1978) The evolution of group territorial behavior and cooperative breeding. *The American Naturalist* 112: 1091–1100.

Gillespie JH (1977) Natural selection for variances in offspring numbers: A new evolutionary principle. *The American Naturalist* 111: 1010–1014.

Gillespie JH (1991) *The Causes of Molecular Evolution*. Oxford University Press.

Giraldeau LA and Caraco T (1993) Genetic relatedness and group size in an aggregation economy. *Evolutionary Ecology* 7: 429–438.

Giraldeau LA and Caraco T (2000) *Social Foraging Theory*. Princeton, NJ: Princeton University Press.

Gonzalez J-CT, Sheldon BC, and Tobias JA (2013) Environmental stability and the evolution of cooperative breeding in hornbills. *Proceedings of the Royal Society Biological Sciences Series B* 280: 20131297.

Griesser M, Drobniak SM, Nakagawa S, and Botero CA (2017) Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biology* 15: e2000483.

Guindre-Parker S and Rubenstein DR (2020) Survival benefits of group living in a fluctuating environment. *The American Naturalist* 195: 1027–1036.

Hamilton WD (1964) The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7: 1–16.

Hatchwell BJ and Komdeur J (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* 59: 1079–1086.

Heg D, Bachar Z, Brouwer L, and Taborsky M (2004) Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 271: 2367–2374.

Heg D, Heg-Bachar Z, Brouwer L, and Taborsky M (2008) Experimentally induced helper dispersal in colonially breeding cooperative cichlids. *Environmental Biology of Fishes* 83: 191–206.

Higashi M and Yamamura N (1993) What determines animal group size– Insider-outsider conflict and its resolution. *The American Naturalist* 142: 553–563.

Jetz W and Rubenstein DR (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology* 21: 72–78.

Keller L and Reeve HK (1994) Partitioning of reproduction in animal societies. *Trends in Ecology & Evolution* 9: 98–102.

Kerr NZ, Morris WF, and Walters JR (2024) Inclusive fitness may explain some but not all benefits derived from helping behavior in a cooperatively breeding bird. *The American Naturalist* 203: 393–410.

Koenig WD (1981) Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *The American Naturalist* 117: 421–443.

Koenig WD and Mumme RL (1987) *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton, N. J.: Princeton University Press.

Koenig WD and Pitelka FA (1981) Ecological factors and kin selection in the evolution of cooperative breeding in birds. In: Alexander RD and Tinkle DW (eds.) *Natural Selection and Social Behavior: Recent Research and New Theory*. New York: Chiron Press.

Koenig WD and Walters EL (2015) Temporal variability and cooperative breeding: Testing the bet-hedging hypothesis in the acorn woodpecker. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 282: 20151742.

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, and Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67: 111–150.

Koenig WD, Walters EL, and Haydock J (2011) Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. *The American Naturalist* 178: 145–158.

Kokko H (2007) Cooperative behaviour and cooperative breeding: What constitutes an explanation? *Behavioural Processes* 76: 81–85.

Kokko H and Ekman J (2002) Delayed dispersal as a route to breeding: Territorial inheritance, safe Havens, and ecological constraints. *The American Naturalist* 160: 468–484.

Kokko H and Lundberg P (2001) Dispersal, migration, and offspring retention in saturated habitats. *The American Naturalist* 157: 188–202.

Kokko H, Johnstone RA, and Wright J (2002) The evolution of parental and alloparental effort in cooperatively breeding groups: When should helpers pay to stay? *Behavioral Ecology* 13: 291–300.

Komdeur J (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358: 493–495.

Krause J and Ruxton GD (2002) *Living in Groups*. Oxford: Oxford University Press.

Lin Y-H, Chan S-F, Rubenstein DR, Liu M, and Shen S-F (2019) Resolving the paradox of environmental quality and sociality: The ecological causes and consequences of cooperative breeding in two lineages of birds. *The American Naturalist* 194: 207–216.

Lin Y-H, Chen Y-Y, Rubenstein DR, Liu M, Liu M, and Shen S-F (2023) Environmental quality mediates the ecological dominance of cooperatively breeding birds. *Ecology Letters* 26: 1145–1156.

Liu M, Chan S-F, Rubenstein DR, Sun S-J, Chen B-F, and Shen S-F (2020) Ecological transitions in grouping benefits explain the paradox of environmental quality and sociality. *The American Naturalist* 195: 818–832.

Lukas D and Clutton-Brock T (2017) Climate and the distribution of cooperative breeding in mammals. *Royal Society Open Science* 4: 160897.

Martin JS, Ringen EJ, Duda P, and Jaeggi AV (2020) Harsh environments promote alloparental care across human societies. *Proceedings of the Royal Society B* 287. 20200758.

Mumme RL (1997) A bird-eye view of mammalian cooperative breeding. In: Solomon NG and French JA (eds.) *Cooperative Breeding in Mammals*. Cambridge: Cambridge University Press.

Nelson-Flower MJ, Wiley EM, Flower TP, and Ridley AR (2018) Individual dispersal delays in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue for dominance. *Journal of Animal Ecology* 87: 1227–1238.

Orr HA (2009) Fitness and its role in evolutionary genetics. *Nature Reviews Genetics* 10: 531–539.

Pen I and Weissing FJ (2000) Towards a unified theory of cooperative breeding: The role of ecology and life history re-examined. *Proceedings of the Royal Society B: Biological Sciences* 267: 2411–2418.

Pruett-Jones SG and Lewis MJ (1990) Sex-ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* 348: 541–542.

Reeve HK (1998) In: Dugatkin L and Reeve HK (eds.) *Game Theory and Animal Behavior*, pp. 118–145. Oxford University Press.

Reyer HU (1990) Pied kingfishers: Ecological causes and reproductive consequences of cooperative breeding. In: Stacey PB and Koenig WD (eds.) *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*, pp. 527–557. Cambridge: Cambridge University Press.

Reyer H-U and Westerterp K (1985) Parental energy expenditure: A proximate cause of helper recruitment in the pied kingfisher (*Ceryle rudis*). *Behavioral Ecology and Sociobiology* 17: 363–369.

Rubenstein DR (2011) Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proceedings of the National Academy of Sciences of the United States of America* 108: 10816–10822.

Rubenstein DR and Abbot P (2017a) *Comparative Social Evolution*. Cambridge: Cambridge University Press.

Rubenstein DR and Abbot P (2017b) The evolution of social evolution. In: Rubenstein DR and Abbot P (eds.) *Comparative Social Evolution*. Cambridge: Cambridge University Press.

Rubenstein DR and Lovette IJ (2007) Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology* 17: 1414–1419.

Selander RK (1964) Speciation in wrens of the genus campylorhynchus. *University of California Publications in Zoology* 74: 1–224.

Shah SS and Rubenstein DR (2023) Group augmentation underlies the evolution of complex sociality in the face of environmental instability. *Proceedings of the National Academy of Sciences USA* 120. e2212211120.

Shen S-F, Emlen ST, Koenig WD, and Rubenstein DR (2017) The ecology of cooperative breeding behaviour. *Ecology Letters* 20: 708–720.

Silk JB (2007) The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 362: 539–559.

Smith JNM (1990) Summary. In: Stacey PB and Koenig WD (eds.) *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*. Cambridge: Cambridge University Press.

Stacey PB and Koenig WD (1990) *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*. Cambridge: Cambridge University Press.

Stacey PB and Ligon JD (1987) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding variation in territory quality and group size effects. *The American Naturalist* 130: 654–676.

Stacey PB and Ligon JD (1991) Territory quality and dispersal options in the acorn woodpecker and a challenge to the habitat-saturation model of cooperative breeding. *The American Naturalist* 137: 831–846.

Sun SJ, Rubenstein DR, Chen BF, et al. (2014) Climate-mediated cooperation promotes niche expansion in burying beetles. *eLife* 3: e02440.

Tuljapurkar SD (1982) Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theoretical Population Biology* 21: 114–140.

Walters JR, Copeyon CK, and Carter Iii JH (1992) Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk* 109: 90–97.

Wcislo WT and Tierney SM (2009) The evolution of communal behavior in bees and wasps: An alternative to eusociality. In: Gadau J and Fewell J (eds.) *Organization of Insect Societies from Genome to Sociocomplexity*. Cambridge, M.A: Harvard University Press.

Whitehouse MEA and Lubin Y (2005) The functions of societies and the evolution of group living: Spider societies as a test case. *Biological Reviews* 80: 347–361.

Wilson EO (1990) *Success and Dominance in Ecosystems: The Case of the Social Insects*. Oldendorf/Luhe: Federal Republic of Germany, Ecology Institute.

Wilson EO (2012) *The Social Conquest of Earth*. New York: Liveright.

Woolfenden GE and Fitzpatrick JW (1984) *The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird*. Princeton: Princeton University Press.

Zack S (1990) Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology* 86: 265–286.