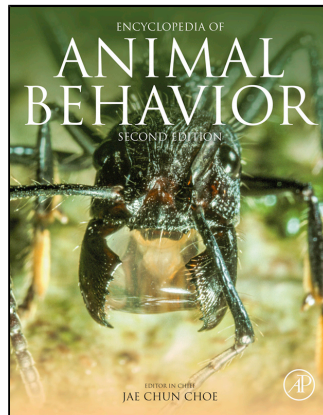


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Environmental Uncertainty and Social Behavior

Sheng-Feng Shen, Biodiversity Research Center, Academia Sinica, Taipei, Taiwan

Dustin R Rubenstein, Columbia University, New York, NY, United States

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Glossary

Cooperative breeding A form of social system in which more than two individuals care for your 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.

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

Animals of nearly every species on earth interact socially during their lifetimes. These interactions can vary from simply coming together only to procreate to the formation of long-term social bonds in group-living species. The term social behavior describes these positive and negative interactions between individuals. When either 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, and what factors drive animal social evolution. This article will address both of these questions by focusing on the role of environmental factors in driving animal social behavior. 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 of all group members are considered, the grouping benefits – group productivity must be greater than the sum of the expected direct fitness of each group member if each individual were to breed on its own – will be 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 the their parents’ offspring (their siblings) from subsequent breeding attempts (Koenig and Mumme, 1987a). 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 solitary yields greater fitness (i.e., solitary breeders usually have the highest per capita productivity) (Selander, 1964). The key insight of this 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, 1987b). 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 harsh 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 more recently have researchers begun 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 above the species level because numerous species seemingly face equally strong ecological constraints but do not exhibit delayed dispersal (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; Higashi and Yamamura, 1993; Giraldeau and Caraco, 2000). 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-piscivorous 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) 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 (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

To solve the paradox of environmental quality and sociality, we argue that one must apply the dual benefits framework and distinguish between the different types of grouping benefits. 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), the adaptive significance of sociality at the intraspecific level remains a difficult question to answer. The dual benefit framework, which provides two fundamental types of grouping benefits that select for sociality, 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 understanding which types of benefits 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 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 benefit 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; and (2) two different types of grouping benefits are clearly distinguished in the dual benefits framework, 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.

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 the "group benefits" as benefits of remaining 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.

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. Determining the relative importance of the two types of benefits requires conducting separate experiments manipulating each type of benefit in the same species

<i>Grouping benefit</i>	<i>Critical experiment</i>	<i>Predicted results</i>	<i>Species</i>	<i>Reference</i>
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)
Collective action	Increase critical resource within the control of existing cooperative social groups.	Larger proportion of young delay dispersal	Cichlid fishes (<i>N. pulcher</i>)	Heg et al. (2008)
	Reduce critical resource within the control of existing cooperative social groups.	Smaller proportion of young delay dispersal	Hover wasps	Field et al. (1998)
	Increase the importance of collective action benefit by manipulating critical ecological environment.	Larger proportion of young delay dispersal	Carrion crows	Baglione et al. (2006)
	Decrease the importance of collective action benefit by manipulating critical ecological environment.	Smaller proportion of young delay dispersal	Western bluebirds	Dickinson and McGowan (2005)
	Manipulate group size and/or composition.	Effects depend on magnitude of the collective action benefit	White fronted bee-eaters	Emlen (1982) , Emlen (1990) , Emlen and Wrege (1991)
			Pied kingfishers	Reyer (1990)
		Sociable weavers	Covas et al. (2004)	
		Cichlid fishes (<i>N. pulcher</i>)	Heg et al. (2004)	
		grey-crowned babblers	Brown et al. (1982)	
		Siberian jays	Ekman and Griesser (2002)	
		Cichlid fishes (<i>N. pulcher</i>)	Heg et al. (2004)	
		Hover wasps	Field et al. (2000)	

Note: After Shen, S.-F., Emlen, S.T., Koenig, W.D., Rubenstein, D.R., 2017. The ecology of cooperative breeding behaviour. Ecology Letters 20, 708–720.

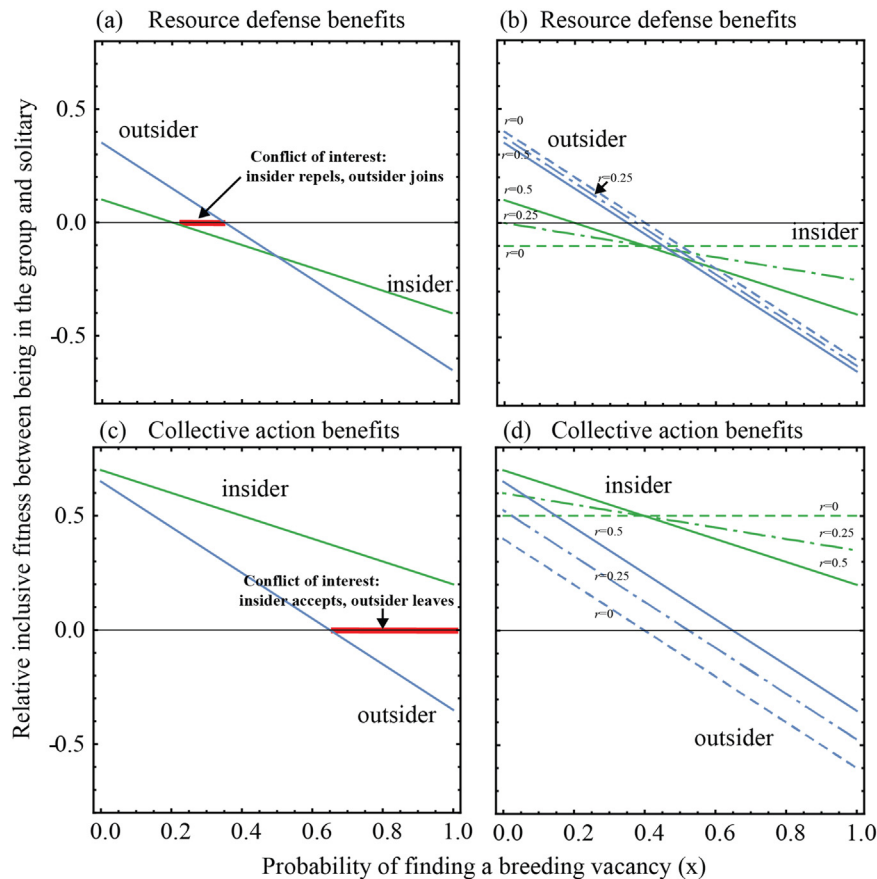


Fig. 1 The relationship between relative inclusive fitness of being in the group versus being solitary for an outsider (blue line, from inequality A1), and of an insider accepting versus rejecting the outsider (green line, from inequality A2). In some cases, a joining outsider *decreases* the direct fitness of the insider ($G_i=0.9$, $L=1$, $r=0.5$, $G_o=0.4$), 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 ($G_i=1.5$, $L=1$, $G_o=0.4$), 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, S.T., Koenig, W.D., Rubenstein, D.R., 2017. The ecology of cooperative breeding behaviour. *Ecology Letters* 20, 708–720.

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 fitnesses 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 a 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 – still influences 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.

Environmental Fluctuation and Sociality

The dual benefits framework suggests that delayed dispersal is not the reason that all cooperatively breeding groups form. As the ecological constraints 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, 1991, 1977; 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 territory, 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 benefits in cooperatively breeding pied kingfishers (*Ceryle rudis*) living in temporally stable but spatially different Rift Valley lake environments where prey availability is unrelated to climatic conditions (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 fluctuating environments, all of which generally emphasize CA benefits in harsh conditions or in fluctuating environments. 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, 1987b; Koenig *et al.*, 2011). Thus, if cooperation only provides benefits in harsh environments, we expect that the variance in fitness will decrease. However, whether the mean fitness will increase or decrease depends on the fitness impact of cooperation in benign environments, something that remains unclear in many organisms. In contrast, the “fission-fusion hypothesis” proposes that individuals adjust their breeding group size to current environmental conditions – forming larger groups in bad years to obtain CA benefits in harsh condition but becoming solitary or forming smaller groups in benign 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 a 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 (Koenig and Walters, 2015; Rubenstein, 2011; Nelson-Flower *et al.*, 2018), additional studies are needed to explore these ideas.

Finally, these alternative hypotheses are often summarized as emphasizing the relative importance of environmentally-driven mean versus variance in fitness for cooperative breeders (Rubenstein, 2011). Interestingly, 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. 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 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, a 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 as well as potential joins, and species that live in both harsh, unpredictable as well as stable, benign environments. 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 will not only help explain why particular species breed cooperatively, but it also enables us to address novel questions such as whether the ecological (e.g., host and species distributional ranges) and evolutionary consequences (e.g., diversification rates in social and non-social lineages) of sociality differ in RD and CA benefit species (Brooks *et al.*, 2017; Sun *et al.*, 2014; Wilson, 2012, 1990). Given the critical role of environmental fluctuation in social evolution, studying the past history and current grouping benefits of social species will also provide crucial insights into how future global climate change will shape the fate of social organisms, including our own species.

References

- Baglione, V., Marcos, J.M., Canestrari, D., *et al.*, 2005. Does year-round territoriality rather than habitat saturation explain delayed natal dispersal and cooperative breeding in the carrion crow? *J. Anim. Ecol.* 74, 842–851.
- Baglione, V., Canestrari, D., Marcos, J.M., Ekman, J., 2006. Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. *Proc. R. Soc. Lond. B Biol. Sci.* 273, 1529–1535.
- Bergmler, R., Heg, D., 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, H.J., 1997. Cooperative breeding in wasps and vertebrates: The role of ecological constraints. In: Choe, J.C., Crespi, B.J. (Eds.), *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge.
- Brooks, K.C., Maia, R., Duffy, J.E., Hultgren, K.M., Rubenstein, D.R., 2017. Ecological generalism facilitates the evolution of sociality in snapping shrimps. *Ecology Letters* 20, 1516–1525.
- Brown, J.L., 1964. The evolution of diversity in avian territorial systems. *The Wilson Bulletin* 76, 160–169.
- Brown, J.L., 1974. Alternate routes to sociality in jays-with a theory for the evolution of altruism and communal breeding. *American Zoologist* 14, 63–80.
- Brown, J.L., 1987. *Helping and Communal Breeding in Birds*. Princeton University Press, Princeton.
- Brown, J.L., Brown, E.R., Brown, S.D., Dow, D.D., 1982. Helpers: Effects of experimental removal on reproductive success. *Science* 215, 421–422.
- Cockburn, A., Russell, A.F., 2011. Cooperative breeding: A question of climate? *Current Biology* 21, R195–R197.
- Cornwallis, C.K., Botero, C.A., Rubenstein, D.R., *et al.*, 2017. Cooperation facilitates the colonization of harsh environments. *Nature Ecology & Evolution* 1, 0057.
- Covas, R., Doutrelant, C., du Plessis, M.A., 2004. Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 827–832.
- Covas, R., 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.
- Darwin, C., 1859. *On the Origin of Species by Means of Natural Selection*. Murray, London.
- Dey, C.J., O'connor, C.M., Wilkinson, H., *et al.*, 2017. Direct benefits and evolutionary transitions to complex societies. *Nature Ecology & Evolution* 1, 0137.
- Dickinson, J.L., McGowan, A., 2005. Winter resource wealth drive's delayed dispersal and family-group living in western bluebirds. *Proc. R. Soc. Lond. B Biol. Sci.* 272, 2423–2428.
- Dickinson, J.L., Hatchwell, B.J., 2004. Fitness consequences of helping. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Ekman, J.A.N., Dickinson, J.L., Hatchwell, B., Griesser, M., 2004. Delayed dispersal. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Ekman, J., Griesser, M., 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proc. R. Soc. Lond. B Biol. Sci.* 269, 1709–1714.
- Emlen, S.T., 1990. White-fronted bee-eaters: helping in a colonially nesting species. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*. Cambridge University Press, Cambridge, pp. 487–526.
- Emlen, S.T., 1982b. The evolution of helping I. An ecological constraints model. *The American Naturalist* 119, 29–39.
- Emlen, S.T., 1984. Cooperative breeding in birds and mammals. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*, second ed. Blackwell Science, Oxford.
- Emlen, S.T., 1991. Evolution of cooperative breeding in birds and mammals. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*, third ed. Blackwell Science, Oxford.
- Emlen, S.T., 1994. Benefits, constraints and the evolution of the family. *Trends in Ecology & Evolution* 9, 282–284.
- Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215–223.
- Emlen, S.T., 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.
- Field, J., Foster, W., Shreeves, G., Sumner, S., 1998. Ecological constraints on independent nesting in facultatively eusocial hover wasps. *Proc. R. Soc. Lond. B Biol. Sci.* 265, 973–977.
- Field, J., Shreeves, G., Sumner, S., Casiraghi, M., 2000. Insurance-based advantage to helpers in a tropical hover wasp. *Nature* 404, 869–871.
- Gaston, A.J., 1978. The evolution of group territorial behavior and cooperative breeding. *The American Naturalist* 112, 1091–1100.
- Gillespie, J.H., 1977. Natural selection for variances in offspring numbers: A new evolutionary principle. *The American Naturalist* 111, 1010–1014.
- Gillespie, J.H., 1991. *The Causes of Molecular Evolution*. Oxford University Press.
- Giraldeau, L.A., Caraco, T., 1993. Genetic relatedness and group size in an aggregation economy. *Evol. Ecol.* 7, 429–438.

- Giraldeau, L.A., Caraco, T., 2000. *Social Foraging Theory*. Princeton University Press, Princeton, NJ.
- Gonzalez, J.-C.T., Sheldon, B.C., Tobias, J.A., 2013. Environmental stability and the evolution of cooperative breeding in hornbills. *Proceedings of the Royal Society Biological Sciences Series B* 280, 20131297.
- Griesser, M., Drobnik, S.M., Nakagawa, S., Botero, C.A., 2017. Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biology* 15, e2000483.
- Hamilton, W.D., 1964. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7, 1–16.
- Hatchwell, B.J., 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., Taborsky, M., 2004. Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 2367–2374.
- Heg, D., Heg-Bachar, Z., Brouwer, L., Taborsky, M., 2008. Experimentally induced helper dispersal in colonially breeding cooperative cichlids. *Environ. Biol. Fishes* 83, 191–206.
- Higashi, M., Yamamura, N., 1993. What determines animal group size—insider-outsider conflict and its resolution. *Am. Nat.* 142, 553–563.
- Jetz, W., Rubenstein, D.R., 2011b. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology* 21, 72–78.
- Keller, L., Reeve, H.K., 1994. Partitioning of reproduction in animal societies. *Trends in Ecology & Evolution* 9, 98–102.
- Koenig, W.D., 1981. Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *The American Naturalist* 117, 421–443.
- Koenig, W.D., Mumme, R.L., 1987a. *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton University Press, Princeton, N. J.
- Koenig, W.D., Mumme, R.L., 1987b. *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton University Press.
- Koenig, W.D., Pitelka, F.A., 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. In: Alexander, R.D., Tinkle, D.W. (Eds.), *Natural Selection and Social Behavior: Recent Research and New Theory*. Chiron Press, New York.
- Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L., Stanback, M.T., 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67, 111–150.
- Koenig, W.D., Walters, E.L., 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, W.D., Walters, E.L., 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., 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., Johnstone, R.A., 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.
- Kokko, H., Lundberg, P., 2001. Dispersal, migration, and offspring retention in saturated habitats. *The American Naturalist* 157, 188–202.
- 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., Ruxton, G.D., 2002. *Living in Groups*. Oxford University Press, Oxford.
- Lukas, D., Clutton-Brock, T., 2017. Climate and the distribution of cooperative breeding in mammals. *Royal Society Open Science* 4, 160897.
- Mumme, R.L., 1997. A bird-eye view of mammalian cooperative breeding. In: Solomon, N.G., French, J.A. (Eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge.
- Nelson-Flower, M.J., Wiley, E.M., Flower, T.P., Ridley, A.R., 2018. Individual dispersal delays in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue for dominance. *Journal of Animal Ecology*. <https://doi.org/10.1111/1365-2656.12814>.
- Orr, H.A., 2009. Fitness and its role in evolutionary genetics. *Nature Reviews Genetics* 10, 531–539.
- Pen, I., Weissing, F.J., 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, S.G., Lewis, M.J., 1990. Sex-ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* 348, 541–542.
- Reeve, H.K., 1998. In: Dugatkin, L., Reeve, H.K. (Eds.), *Game Theory and Animal Behavior*. Oxford University Press, pp. 118–145.
- Reyer, H.U., 1990. Pied kingfishers: ecological causes and reproductive consequences of cooperative breeding. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*. Cambridge University Press, Cambridge, pp. 527–557.
- Rubenstein, D.R., 2011b. 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, D.R., Abbot, P., 2017a. *Comparative Social Evolution*. Cambridge University Press, Cambridge.
- Rubenstein, D.R., Abbot, P., 2017b. The evolution of social evolution. In: Rubenstein, D.R., Abbot, P. (Eds.), *Comparative Social Evolution*. Cambridge University Press, Cambridge.
- Rubenstein, D.R., Lovette, I.J., 2007. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology* 17, 1414–1419.
- Selander, R.K., 1964. *Speciation in Wrens of the Genus Campylorhynchus*, 74. University of California Publications in Zoology, pp. 1–224.
- Shen, S.-F., Emlen, S.T., Koenig, W.D., Rubenstein, D.R., 2017. The ecology of cooperative breeding behaviour. *Ecology Letters* 20, 708–720.
- Silk, J.B., 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362, 539–559.
- Smith, J.N.M., 1990. Summary. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*. Cambridge University Press, Cambridge.
- Stacey, P.B., Koenig, W.D., 1990. *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*. Cambridge University Press, Cambridge.
- Stacey, P.B., Ligon, J.D., 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, P.B., Ligon, J.D., 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, S.J., Rubenstein, D.R., Chen, B.F., et al., 2014. Climate-mediated cooperation promotes niche expansion in burying beetles. *eLife* 3, e02440.
- Tuljapurkar, S.D., 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theoretical Population Biology* 21, 114–140.
- Walters, J.R., Copeyon, C.K., Carter III, J.H., 1992. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk* 109, 90–97.
- Wcislo, W.T., Tierney, S.M., 2009. The evolution of communal behavior in bees and wasps: An alternative to eusociality. In: Gadau, J., Fewell, J. (Eds.), *Organization of Insect Societies from Genome to Sociocomplexity*. Harvard University Press, Cambridge, MA.
- Whitehouse, M.E.A., 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, E.O., 1990. *Success and Dominance in Ecosystems: The Case of the Social Insects*. Oldendorf/Luhe, Federal Republic of Germany, Ecology Institute.
- Wilson, E.O., 2012. *The Social Conquest of Earth*. Liveright, New York.
- Woolfenden, G.E., Fitzpatrick, J.W., 1984. *The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird*. Princeton University Press, Princeton.
- Zack, S., 1990. Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology* 86, 265–286.