

**IDEA AND
PERSPECTIVE**

The ecology of cooperative breeding behaviour

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Abstract

Ecology is a fundamental driving force for the evolutionary transition from solitary living to breeding cooperatively in groups. However, the fact that both benign and harsh, as well as stable and fluctuating, environments can favour the evolution of cooperative breeding behaviour constitutes a paradox of environmental quality and sociality. Here, we propose a new model – the dual benefits framework – for resolving this paradox. Our framework distinguishes between two categories of grouping benefits – resource defence benefits that derive from group-defended critical resources and collective action benefits that result from social cooperation among group members – and uses insider–outsider conflict theory to simultaneously consider the interests of current group members (insiders) and potential joiners (outsiders) in determining optimal group size. We argue that the different grouping benefits realised from resource defence and collective action profoundly affect insider–outsider conflict resolution, resulting in predictable differences in the *per capita* productivity, stable group size, kin structure and stability of the social group. We also suggest that different types of environmental variation (spatial vs. temporal) select for societies that form because of the different grouping benefits, thus helping to resolve the paradox of why cooperative breeding evolves in such different types of environments.

Keywords

bet hedging, ecological constraint, environmental uncertainty, fluctuating selection, group living, group size, insider–outsider conflict, social evolution, sociality.

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INTRODUCTION

Understanding how cooperation evolves is central to explaining one of the major evolutionary transitions in life – the process describing how biological entities such as single cells or individuals merge as part of a larger unit to become a multicellular organism or form a collective such as a cooperatively breeding group, a social system in which more than two individuals care for young (Maynard Smith & Szathmari 1995; Bourke 2011; Calcott & Sterelny 2011; West *et al.* 2015). A key driving force in the transition from living solitarily to breeding cooperatively is the generation of kin structure, or high within-group relatedness (Hamilton 1964; Boomsma 2009; Cornwallis *et al.* 2010; Lukas & Clutton-Brock 2012). However, kinship alone does not explain the evolution of sociality (Hamilton 1964). Indeed, numerous theoretical and empirical studies since Hamilton's seminal work have demonstrated the central role that ecology plays in shaping the evolution of sociality and cooperation more broadly (Queller & Strassmann 1998; Korb & Heinze 2008; Bourke 2011; Purcell 2011). Yet despite decades of work, the role that ecology plays in driving the transition from solitary living to breeding cooperatively remains poorly understood.

The evolution of cooperative breeding behaviour occurs in, and is apparently favoured by (Liu *et al.* unpubl. manuscript), benign and harsh environments (Soucy & Danforth 2002; Avilés *et al.* 2007; Gonzalez *et al.* 2013), as well as in stable and fluctuating environments (Grimes 1976; Ford *et al.* 1988; Jeanne 1991; DuPlessis *et al.* 1995; Kaspari & Vargo 1995; Rubenstein & Lovette 2007; Jetz & Rubenstein 2011; Lukas & Clutton-Brock 2017). These seemingly inconsistent biogeographic patterns create a paradox of environmental quality and sociality that has made it difficult to understand the role of ecology in shaping sociality at broad taxonomic and geographic scales. Moreover, because many vertebrate cooperatively breeding groups (hereafter CBGs) form through the retention of offspring, hypotheses underlying the evolution of vertebrate social behaviour have often restricted their focus upon the decision of offspring to delay dispersal and remain in their parental group rather than disperse and attempt to breed independently (Emlen & Vehrencamp 1983; Dickinson & Hatchwell 2004).

The formation of CBGs in birds and mammals is traditionally explained by the ecological constraints hypothesis, which argues that grown young delay dispersal when ecological constraints severely lower the expected fitness payoffs of

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alternative options, either dispersing to breed independently or floating until a breeding vacancy arises (Brown 1974; Koenig 1981; Emlen 1982, 1994; Koenig *et al.* 1992; Hatchwell 2009). The ecological constraints hypothesis has played an important role in explaining not only the evolution of many CBGs but also in describing their stability and underlying social dynamics (Emlen 1991, 1995, 1997). However, the predictive power of the ecological constraints hypothesis has been questioned (Cockburn 1998; Hatchwell 2016) – particularly at the interspecific level – for at least three reasons. First, numerous species, even in the same environment as cooperatively breeding ones, seemingly face equally strong ecological constraints, yet do not exhibit delayed dispersal of offspring or alloparental care behaviour (Smith 1990; Koenig *et al.* 1992; Brockmann 1997; Hatchwell & Komdeur 2000; Kokko & Lundberg 2001; Covas & Griesser 2007; Kokko 2007). Second, the pattern across all birds (Jetz & Rubenstein 2011) and mammals (Lukas & Clutton-Brock 2017) that cooperatively breeding species are more common in environments with high interannual variation in rainfall poses a challenge to the ecological constraints hypothesis because habitat saturation should be less likely to occur in such highly variable environments (Cockburn & Russell 2011). Third, intraspecific variation in kin structure among CBGs resulting from processes other than delayed dispersal by offspring is common (Riehl 2013). Thus, hypotheses that only address delayed dispersal by offspring fail to capture all of the factors that influence group formation in many cooperatively breeding species. There is therefore a need to expand the classically accepted ecologically driven theoretical framework of cooperative breeding to incorporate the role of environmental variation in not just space but also time. This framework must also encompass CBGs that form not just from delayed dispersal but through the acceptance of non-natal individuals that may or may not be genetic relatives, including ‘redirected helping’, when failed breeders switch to helping other individuals (Emlen 1990; Hatchwell *et al.* 2004; Cockburn & Russell 2011; Cockburn 2013; Hatchwell 2016; Shen *et al.* 2016).

Here, we propose a new theoretical framework, referred to as the *dual benefits framework*, for studying the evolution of cooperative breeding behaviour in social vertebrates, including the full spectrum of societies from singular to plural breeding, and even eusociality. In contrast to previous hypotheses that focus solely upon delayed dispersal (Emlen & Vehrencamp 1983; Dickinson & Hatchwell 2004), we argue that a more predictive framework for the evolution of cooperative breeding behaviour must consider group formation from the perspectives of both current group members and potential joiners, including offspring potentially remaining in the natal group and non-kin immigrants. This approach is necessary because conflict over group formation, referred to as *insider–outsider conflict* often exists between current group members (the insiders) and potential joiners (the outsiders), even when they are closely related (Giraldeau & Caraco 1993, 2000; Higashi & Yamamura 1993). Importantly, outsiders include not only individuals from other groups considering joining a particular focal group but also potential dispersers (i.e. offspring born in that group) deciding whether to remain in their natal group or leave and attempt to breed elsewhere.

We begin with the assertion that if the interests of both current group members and potential joiners are considered, a necessary condition for the formation of cooperatively breeding groups is a grouping benefit such that the total group productivity must be greater than the sum of the expected fitnesses of each group member if each individual bred on their own, taking into account changes in long-term genetic contributions due to fluctuating environments. Next, we distinguish between two categories of grouping benefits and suggest ways to do so empirically: (1) *resource defence benefits* (hereafter RD), which are derived from groups defending critical resources; and (2) *collective action benefits* (hereafter CA), which result from social cooperation among group members. We argue that these different grouping benefits profoundly affect the *per capita* productivity, stable group size, kin structure and stability of the resulting social groups. Finally, we incorporate recent theoretical developments linking spatial and temporal patterns of environmental variation into our dual benefits framework because each has different implications for grouping benefits and ultimately for group formation. We argue that spatial variation more strongly influences RD benefits, whereas CA benefits are influenced more by temporal variation. The dual benefit framework thus helps to resolve the paradox of environmental quality and sociality – why the evolution of sociality can be favoured in both harsh, fluctuating and benign, stable environments – and provides an improved predictive framework for studying the evolution of cooperative breeding.

INSIDER–OUTSIDER CONFLICT THEORY AND THE FORMATION OF COOPERATIVELY BREEDING GROUPS

Insider–outsider conflict theory provides a framework for considering not only why groups form but also what the optimal group size should be. In most species, it is in the common interest of insiders to maintain the most productive (or optimal) group size, measured in terms of *per capita* productivity (Giraldeau & Caraco 1993, 2000; Higashi & Yamamura 1993). However, as long as joining the group yields higher fitness than remaining solitary, outsiders will gain a fitness advantage by joining the group, thereby potentially driving group size to become larger than the insiders’ optimal size (Sibly 1983). Therefore, instead of focusing only upon why offspring – a type of potential joiner – remain in the natal territory, the concept of insider–outsider conflict, which considers the perspective of both the offspring and current group residents, provides a more complete framework for understanding not only why CB groups form but also why they vary in size and kinship. Although we acknowledge that there will be some conflict of interest among insiders, we assert that insider interests are more aligned than those of insiders and outsiders. Thus, for simplicity, we assume that insiders have a common interest over group membership. Future models using the dual benefits framework could consider cases when insider interests are less aligned.

We begin by employing Hamilton’s rule to determine whether an individual’s decision to join a group or to breed solitarily will be favoured by natural selection. We consider a two-player

game that includes a single outsider (e.g. offspring) and a single insider (e.g. parent) (see Appendix A for an n-player game). Let G_o be the direct fitness of an outsider joining the natal group and G_i the direct fitness of the insider if the outsider joins the group. In addition, let the direct fitness payoff of being solitary be xL and L for the outsider and insider, respectively, where x denotes the probability of finding a breeding vacancy for a dispersing individual. From the outsider's perspective, joining the group will be favoured over leaving if

$$G_o + rG_i > xL + rL \quad (\text{A1})$$

where r is the coefficient of relatedness between the insider and the outsider. Similarly, from the insider's perspective, allowing the outsider to join in the group will be favoured over repelling the joining outsider if

$$G_i + rG_o > L + rxL \quad (\text{A2})$$

To determine the minimum requirement of G_o for an outsider to prefer joining the group, we rearrange inequality (A1) to obtain

$$G_o > xL + r(L - G_i) \quad (\text{A3})$$

Similarly, the stability condition for the insider to prefer accepting the joining outsider into the group is

$$G_i > L + r(xL - G_o) \quad (\text{A4})$$

Finally, by combing inequalities (A3) and (A4), we can see that the necessary but not sufficient condition for a CBG to form is that the grouping benefit must be greater than the sum of the direct fitnesses of each player if they bred solitarily, which can be described as

$$G_o + G_i > L(x + 1) \quad (\text{A5})$$

It is straightforward to compare these inclusive fitness functions to previous theories for the evolution of CBGs that focused only upon delayed dispersal decision; we do this within our dual benefit framework in Appendix B. For simplicity, we assume that environments are spatially homogeneous, where solitary breeders obtain direct fitness L . For the heterogeneous environment with high and low quality patches, inequality (A5) can still apply (Fig. 1a).

DUAL BENEFITS AND THE FORMATION OF COOPERATIVELY BREEDING GROUPS

Animals can receive a number of direct benefits from living in a group, including gaining access to resources or mates, avoiding predators, providing offspring care and maintaining homeostasis (Alexander 1974; Krause & Ruxton 2002; Rubenstein & Abbot 2017). All of these potential direct benefits can be categorised as either RD or CA grouping benefits. Importantly, RD and CA benefits are not mutually exclusive, and members of CBGs may gain a combination of both. We suspect, however, that in most cases one type of benefit is of considerably greater importance for the formation and maintenance of the group than the other, although the type of grouping benefit that drives group formation need not be the same as the one that helps maintain group living (see Siberian jay example in Appendix C).

The distinction between resource defence and collective action benefits has roots going back at least as far as Alexander's (1974) selective backgrounds of group living, two of which involved CA benefits of individuals gained by the presence of other individuals in the group, and one of which involved RD benefits of individuals gaining '...solely from the presence of some other resource in the immediate environment...'. Subsequent work proposing a similar dichotomy include Emlen's (1982) review pointing out two different forms of ecological constraints potentially limiting personal reproduction in cooperative breeders residing in stable vs. fluctuating environments, Koenig *et al.*'s (1992) delayed dispersal models that made the distinction between 'extrinsic constraints' and 'intrinsic benefits', and Koenig *et al.*'s (2016) recent distinction between 'constraints-based' and 'benefits-based' CBGs. Despite these clear historical antecedents, previous application of these ideas to cooperative breeding behaviour have not recognised many of the essential differences between the two types of benefits, instead focusing only upon explaining the evolution of offspring delayed dispersal. Considering dual grouping benefits from the perspective of both current and potential group members serves to clarify the confusion that has emerged from studies involving a diverse array of cooperatively breeding species (Appendix B).

Resource defence benefits

Resource defence benefits result from the defence of, and familiarity with, critical ecological resources by the group. Such benefits will be especially important if critical resources are defensible by a group either in space or through time. Recent theoretical work that explicitly considers the feedback between demography and the evolution of behaviour has shown that population density and the degree of temporal stability or spatial heterogeneity of patch quality jointly influence offspring dispersal decisions and the evolution of cooperative breeding behaviour (McNamara & Dall 2011; Rodrigues & Johnstone 2014; Avila & Fromhage 2015). RD benefits favour offspring delaying dispersal either in temporally stable environments or in fluctuating environments where the temporal autocorrelation of habitat quality is high, as values of group-defended resources are therefore predictable. The concept of RD benefits assumes that group-controlled resources are fixed in the sense that the action of group members does not increase the quality or quantity of resources accessible to the group. To the extent that actions by group members increase resource quality or quantity, this constitutes a CA benefit (see below).

In a spatially homogenous environment where the variation in resource quality among patches is small, relatively high population density reduces the chances of offspring finding a breeding vacancy, yet does not necessarily lead to delayed dispersal because offspring may still be able to search for breeding vacancies while living away from the natal territory, potentially as 'floaters' (Hamilton & May 1977). Thus, high population density is likely to promote offspring delaying dispersal in homogenous environments when (1) the natal territory is a 'safe haven' where parents allow offspring access to food resources and safe habitat while waiting for breeding

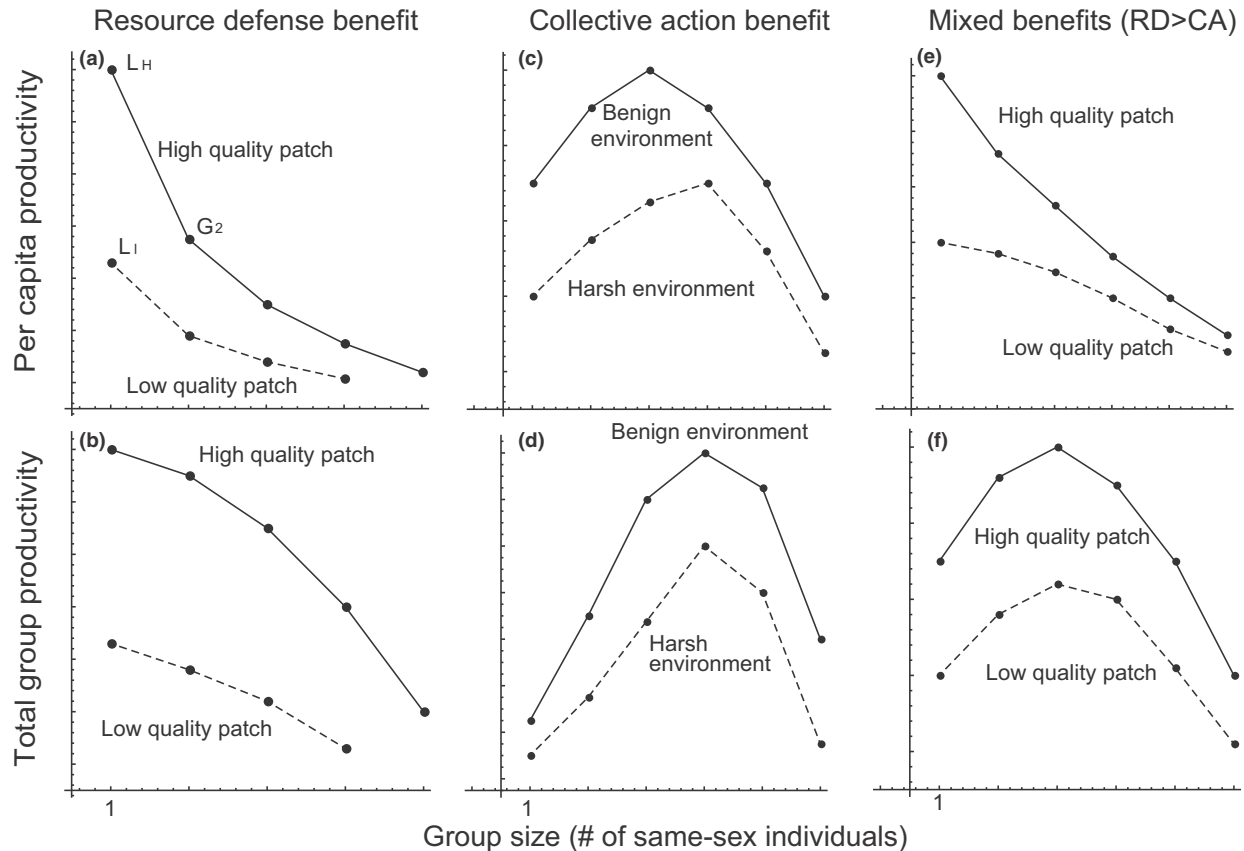


Figure 1 The expected relationship between group size and productivity (in terms of direct fitness) for cooperatively breeding groups that form due to the two types of grouping benefits under benign (temporal) or high-quality (spatial) (solid lines) and harsh (temporal) or low-quality (spatial) environmental conditions (dashed lines). These qualitative predictions are based upon mathematical equations (inequality (A5) in the text and (B11) in Appendix B). In each case, the expected relationship between group size and *per capita* productivity is shown on top, and the relationship between group size and total group productivity is shown below. (a,b) Resource defence (RD) benefits primary; (c,d) collective action (CA) benefits primary; (e,f) benefits are a combination of resource defence and collective action benefits, but the former are relatively more important. In all cases, optimal group size is the size that maximises the insider's absolute *per capita* productivity (i.e. direct fitness). It may seem counterintuitive for individuals to form groups primarily because of resource defence benefits, where *per capita* productivity decreases with group size. However, based upon the simple inclusive calculation derived in the text (inequality (A5)), resource defence benefit groups can only be stable if $2G_2 > L_H + xL_L$, where x is the probability of finding a breeding vacancy, $G_i + G_o = 2G_2$, L_H and L_L represent direct fitness of solitary breeding in high- and low-quality habitats, respectively. In other words, resource defence benefits only occur when breeding vacancies are limited, which is the central idea behind the ecological constraints hypothesis.

opportunities (Kokko & Ekman 2002), or (2) group members (insiders) control access to the critical resources, making it unlikely that individuals will disperse and join a non-natal territory (Shen & Johnstone, unpublished data). In other words, RD benefits are likely to be important in more benign environments, which can result in higher population density and thus lead to higher levels of intraspecific competition (Sun *et al.* 2014; Shen *et al.* 2016).

These two criteria, along with relatively high population density, are likely to apply to many CBGs. For example, in carrion crows, *Corvus corone*, offspring natal philopatry occurred in a year-round territorial Spanish population where population density was lower and vacant territories were common, but not in a central European population where birds frequently abandoned their territories after breeding. Baglione *et al.* (2005) suggested that the key factor driving the difference in natal philopatry between the populations was year-round territoriality rather than high population density and

ecological constraints. However, these results are consistent with the predictions of the RD benefit concept because high population density will not favour delayed dispersal if there are no defendable resources and thus no defendable year-round territories. In contrast, the dual benefits hypothesis is consistent with offspring delayed dispersal occurring in the Spanish crow population given that the environment was spatially heterogeneous, as this would result in offspring born on high-quality territories benefiting by remaining on their natal territory to enjoy its 'safe haven' or queue for inheriting a high-quality patch, even when population density is low (Koenig *et al.* 1992; Komdeur 1992).

Collective action benefits

Collective action benefits arise from active coordination among group members enhancing the efficiency of group activities such as foraging, provisioning, protecting young,

predator detection and deterrence and energy conservation (homeostasis). We exclude benefits arising from passive dilution (selfish herd) effects (Hamilton 1971) because no cooperation or collective behaviour is needed. CA benefits are likely to be most important when local conditions are harsh, as proposed by the ‘hard life hypothesis’ (Koenig & Mumme 1987; Koenig *et al.* 2011) and the ‘temporal variability hypothesis’ (Rubenstein & Lovette 2007; Rubenstein 2011). For example, in species where starvation of young is common due to high environmental variability and unpredictability, significant CA benefits are likely to be derived from additional individuals provisioning young when environmental conditions are poor (Emlen & Wrege 1991; Hatchwell 1999; Cornwallis *et al.* 2009). Similarly, the importance of active group defence of young – another CA benefit – will be greater when predation risk (Austad & Rabenold 1985) or risk of brood parasitism is high (Feeney *et al.* 2013). Therefore, CA benefits can be derived from coping with environmental challenges in both benign and harsh environments (Sun *et al.* 2014; Shen *et al.* 2016), but are likely to be more important in the latter.

Obligate cooperatively breeding species represent extreme cases where CA benefits become mandatory. Avian examples include the critical necessity of multiple caregivers to feed, defend or ‘instruct’ young in white-winged choughs, *Corcorax melanorhamphos* (Heinsohn 1992), chestnut-crowned babbler, *Pomatostomus ruficeps* (Browning *et al.* 2012; Russell 2016), apostlebirds, *Struthidae cinera* (Boland *et al.* 1997), and superb starlings, *Lamprotornis superbus* (Rubenstein 2016), as well as the necessity of a minimum group size for effective deterrence of nest predators in stripe-backed wrens, *Campylorhynchus nuchalis* (Rabenold 1984, 1985) and superb starlings (Rubenstein 2006). Mammalian examples include

predator detection (Clutton-Brock *et al.* 1999) and the necessity of multiple provisioning individuals for offspring survival in meerkats, *Suricata suricatta* (Clutton-Brock *et al.* 2001), the importance of large groups for increased hunting and provisioning efficiency in wild dogs, *Lycaon pictus* (Courchamp *et al.* 2002; Gusset & Macdonald 2010), and cooperative defence against infanticide in African lions, *Panthera leo* (Pusey & Packer 1994).

Distinguishing between types of grouping benefits

Determining the primary grouping benefit for a social species is important because the applicability of insider–outsider conflict theory is different for groups that form primarily due to RD vs. CA benefits. This distinction generates different predictions concerning *per capita* productivity, stable group size and kin structure of the resulting social groups.

A first step in determining the relative importance of RD and CA benefits is to examine the relationship between group size and fitness, which we do with a graphical model (Fig. 1) that is based on a mathematical one presented in Appendix B. Specifically, *per capita* productivity *decreases* with increasing group size when RD benefits are of primary importance, whereas *per capita* productivity *increases* with increasing group size, at least initially, when CA benefits are more important (Fig. 1a,c). The relative importance of the two types of benefits can be confirmed experimentally in ways that we summarise in Table 1. Importantly, these guidelines apply to the current selective factors favouring CBGs, not the factors that originally led to the formation of CBGs. Once such groups exist there will be selection for increased CA benefits, even if they are initially driven entirely by RD benefits (Koenig *et al.* 1992).

Table 1 Summary of critical experiments testing the relative importance of resource defence benefits vs. collective action benefits in the formation and maintenance of CBGs in various cooperative breeding species discussed in the text. Determining the relative importance of the two types of benefits requires conducting separate experiments manipulating each type of benefit in the same species.

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

Resource defence benefits primary

Productivity in a CBG for which benefits are primarily due to RD is determined by the quality of the resources controlled by the group. However, both *per capita* and total group productivity will *decrease* as group size increases because the fixed quantity of defended resources must be shared among more individuals (Fig. 1a,b). Additional group members can increase group productivity only through behaviours that constitute CA benefits. Thus, many CBGs for which RD is a major grouping benefit also gain CA benefits. However, when *only* RD benefits apply, the optimal group size – that which yields the highest *per capita* productivity – will be a non-cooperatively breeding group of two individuals (Koenig 1981).

The best way to confirm the primacy of RD benefits is to manipulate critical resources controlled by groups or, alternatively, to experimentally create critical resources outside the control of the group (Table 1). If RD provides the primary benefit of grouping, such resource manipulations should lead to predictable changes in the observed size of manipulated vs. unmanipulated (control) groups. Examples of experimental studies confirming the primary importance of RD benefits through the experimental addition of critical resources include the translocation of birds to previously unoccupied habitat in Seychelles warblers, *Acrocephalus sechellensis* (Komdeur 1992), the construction of artificial nesting cavities in previously unoccupied areas for red-cockaded woodpeckers, *Picoides borealis* (Walters *et al.* 1992), and the creation of breeding vacancies by experimental removal of breeding pairs in superb fairy-wrens, *Malurus cyaneus* (Pruett-Jones & Lewis 1990). In each of these species, the creation of new, high-quality resources (or breeding vacancies in the case of fairy-wrens) caused individuals to leave their current social group and reproduce solitarily. Similarly, experimental reduction in critical winter resources (mistletoe) within the control of groups of western bluebirds, *Sialia mexicana*, caused group size to decrease because more sons dispersed from their natal groups in depleted relative to control groups (Dickinson & McGowan 2005). In an analogous experiment with carrion crows in Spain, increasing critical resources within control of groups by providing supplemental food year-round caused group size to increase relative to control groups because more juveniles remained in their natal groups on food supplemented territories (Baglione *et al.* 2006).

Collective action benefits primary

The optimal group size of CBGs for which benefits are primarily due to CA will always be larger than a solitary breeding pair. How much larger depends upon the magnitude of the CA benefits (Fig. 1c,d). Both total group and *per capita* productivity will increase as group size increases until the latter reaches its optimum, after which *per capita* and eventually total group productivity will decline as group size increases further. Thus, the optimal group size will depend upon the point at which CA benefits are outweighed by the increased costs of social conflict or other automatic costs of group living (Alexander 1974).

The best way to confirm the primacy of CA benefits is to experimentally manipulate their magnitude, which should lead

to predictable changes in the observed group size. CA benefits are often strongly affected by local environmental conditions. For example, in both sociable weavers, *Philetairus socius* (Covas *et al.* 2004), and white-fronted bee-eaters, *Merops bullockoides* (Emlen 1990), the CA benefit from group provisioning of nestlings is more important in dry years when insect abundance is lower. As predicted from our models, breeding group size (i.e. the number of helpers per nest) was significantly larger in dry years than in wet years for both species (Emlen 1982, 1990; Covas *et al.* 2004). Moreover, fledgling success in both species increased with increasing group size because nestling starvation declined, an effect that was most pronounced when conditions were harshest (Emlen 1990; Emlen & Wrege 1991; Emlen *et al.* 1991; Covas *et al.* 2008). In addition, providing supplemental food to sociable weavers prior to and during the breeding season reduced the CA benefit of larger groups in caring for young in supplemented relative to control colonies (Covas *et al.* 2004). As predicted, this resulted in a decrease in breeding group size and an increase in the proportion of individuals attempting to breed independently (Covas & du Plessis 2005).

Summary

The predicted responses to experimental food supplementation experiments are opposite for groups in which CA vs. RA benefits are of primary importance. This can be seen in the parallel experiments in sociable weavers, where enhancing resources resulted in a decrease in delayed dispersal (Covas *et al.* 2004), compared to carrion crows, where enhancing resources resulted in an increase in delayed dispersal and helping behaviour (Baglione *et al.* 2006) (Table 1). Finally, when manipulations indicate that *both* RD and CA benefits are important, further interpretation is required to assign the primacy of benefit type (see examples in Appendix C).

LINKING INSIDER–OUTSIDER CONFLICT THEORY AND THE DUAL BENEFITS FRAMEWORK

Considering the formation of CBGs from the perspectives of both current group members and potential joiners allows us to employ insider–outsider conflict theory to predict group size and kinship variation in CBGs (Giraldeau & Caraco 1993, 2000; Higashi & Yamamura 1993). Interestingly, if the resolution of insider–outsider conflict is explicitly considered without assuming who has control over group membership, the model predicts that the individual(s) whose direct fitness gains or losses are most pronounced will have greater influence on optimal group size (Appendix D). This occurs because direct fitness gains or losses of different individual behavioural decisions (e.g. accepting vs. repelling, or joining vs. leaving) impact the relative *inclusive* fitness differences between insiders and outsiders. In other words, if insiders suffer more direct fitness losses by the joining of an outsider, they will fight to repel the potential joiner. Likewise, if an outsider will gain in terms of direct fitness by joining the group, it will expend a high level of effort to do so. As a consequence, equilibrium group size will increase as genetic relatedness between insiders and an outsider increases, but only if the direct fitness cost for insiders to accept an

outsider is relatively large, or if the benefit of joining for an outsider is small. Moreover, if there are more insiders than outsiders in the group, as is usually the case, the evolutionarily stable group size will more closely approach that which is optimal for insiders (Appendix D). Thus, we focus further discussion on the scenario where insiders have greater control over group membership than outsiders.

Resource defence benefits and group formation

In cases where RD benefits underlie group formation, there will be few direct fitness benefits for an insider to accept a potential joiner. This is because the optimal breeding group size for a purely RD group is a solitary pair, so groups can never be smaller than the optimal size (Fig. 1a). Increases in group size will always reduce mean *per capita* productivity. The resolution of insider–outsider conflict in this scenario will likely depend upon negative interactions – aggression or eviction – and unrelated outsiders will usually be repelled. However, insiders may still accept a closely related outsider when this addition results in an increase in the *per capita inclusive* fitness of group members (Fig. 2a). Thus, only close genetic relatives should be accepted into resource defence CBGs that are larger than the most productive size (Shen *et al.* unpubl. manuscript; see also Appendix B).

We therefore expect that CBGs gaining primarily RD benefits will consist predominantly of close genetic relatives (Table 2). In addition, CBGs forming primarily for RD benefit will be inherently unstable because all participants will benefit when non-breeding members disperse to occupy limited breeding vacancies elsewhere when they arise (Emlen 1995). As a consequence, CBGs that form because of RD benefits are unstable, even in stable environments.

Collective action benefits and group formation

In cases where CA benefits underlie group formation, *per capita* productivity in groups at optimal size will be higher than

being solitary (Fig. 1c). If current group size is *smaller* than the most productive *per capita* group size, insiders should accept outsiders whether or not they are kin to reach the optimal group size (Fig. 2b). Insiders should prefer genetically related outsiders because the alignment of genetic interests between relatives lowers the expected level of social conflict, thereby increasing total productivity for any given group size. Thus, assuming that insiders have control over group membership, genetically unrelated outsiders will be more likely to join the group if: (1) the fitness gain of the outsider is substantially higher than the inclusive fitness loss of the insiders; (2) the current group size is smaller than the most productive size (Appendix B); and (3) genetically related outsiders are not available to achieve the optimal group size (Shen *et al.* unpubl. manuscript).

Based upon this logic, we predict that CBGs gaining primarily CA benefits will be more variable in their genetic composition and will more frequently include non-kin (Table 2). This is because current group size will often be smaller than the most productive size, potentially resulting in the acceptance of unrelated outsiders. Importantly, this will occur more frequently in temporally fluctuating than in stable environments.

Dual benefits and dispersal

Based upon insider–outsider conflict theory as applied to dual benefit CBGs (Shen *et al.* unpubl. manuscript), we argue that there are two distinctive types of natal philopatry depending upon whether or not group size exceeds the most productive size in terms of *per capita* productivity. Natal philopatry should only be considered as ‘delayed dispersal’ when offspring join their natal group to form a CBG that is larger than the most productive size, as occurs in all purely RD benefit groups and some CA benefit groups. Delayed dispersal is critical for the *formation* of CBGs when they are based entirely upon RD benefits, as found in many singular breeding species with helpers at the nest.

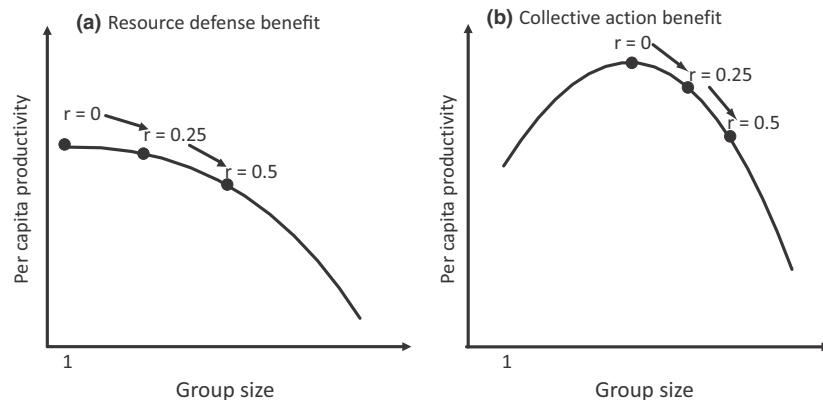


Figure 2 Predictions of insider–outsider conflict resolution theory for cooperatively breeding groups forming by resource defence and collective action benefits. (a) Because insiders gain only indirect fitness by accepting outsiders, larger groups will consist of more closely related individuals when resource defence benefits are the primary driver of cooperatively breeding groups. (b) Because unrelated group members can generate collective action benefits, insiders will accept unrelated joiners until groups reach the most productive *per capita* size, after which only genetically related joiners will be accepted. r = the minimum relatedness required for insiders to maximise inclusive fitness at different stable group sizes. Modified from Giraldeau & Caraco (2000). See also Appendix B for more detailed explanations.

Table 2 Summary of predicted attributes (observed vs. most productive *per capita* group size, kin composition and long-term stability) of cooperatively breeding groups that form primarily for resource defence or collective action benefits, respectively. Modified from Shen *et al.*, unpubl. manuscript.

Attribute	Resource defence benefit	Collective action benefit
Most productive group size	2	≥ 3
Observed mean group size	Larger than most productive group size	Equal to most productive group size
Group composition	Predominantly or exclusively close genetic relatives	Variable but often include non-kin
Long-term stability	Low (all members gain when non-breeders disperse to fill breeding vacancies)	Variable but can be high

In contrast to RD benefit cases, where delayed dispersal is essential for group formation, delayed dispersal is not critical for the formation of CBGs based primarily upon CA benefits. Instead of leading to group formation itself, delayed dispersal can influence group size and kin structure once groups have formed because of CA benefits. A second type of natal philopatry occurs when offspring remain in their natal groups in CA benefit CBGs when group size is smaller than the most productive size. However, dispersal in these cases is not really 'delayed' because staying offspring can increase their own *per capita* productivity and in some cases obtain breeding opportunities, as has been observed in joint-nesting Taiwan yuhinas, *Yuhina brunneiceps* (Shen *et al.* 2016).

Delayed dispersal should therefore be the primary driver of cooperative breeding behaviour when groups form because of RD benefits, but it should only affect group size and kinship composition when groups form initially because of CA benefits. Consequently, determining the primary grouping benefit for a species is important because insider–outsider conflict resolves differently in groups formed primarily because of RD benefits and those that form primarily because of CA benefits (Table 2).

DUAL BENEFITS AND SPATIOTEMPORAL ENVIRONMENTAL VARIATION

Cooperatively breeding species are not only commonly found in temporally fluctuating environments (Jetz & Rubenstein 2011; Lukas & Clutton-Brock 2017), they are also expected to be more common in spatially heterogeneous environments (Stacey & Ligon 1987, 1991; Koenig *et al.* 1992). Here, we explore the relationship between environmental harshness in both time and space and the evolution of cooperative breeding. Importantly, environmental stochasticity potentially changes the reproductive value of offspring born in good or bad years because of fluctuations in population size, which we believe have a profound impact on the evolution of cooperative breeding behaviour (Appendix E).

Dual benefits in temporally stable environments

Although spatial and temporal variability are both causes of environmental variation, they have separate and distinct influences on the evolution of cooperative breeding behaviour (Rubenstein 2016). As we described earlier, spatial environmental variability is an important generator of RD benefits favouring delayed offspring dispersal in a temporally stable environment; RD benefits can also occur in homogeneous environments if insiders control resources. However, the effects of spatial environmental heterogeneity are more complicated in temporally fluctuating environments. If the

temporal autocorrelation of resource quality is higher in high-quality patches – meaning that high- and low-quality patches remain of relatively high and low quality through time, respectively – at least some of the offspring born in high-quality patches will gain an RD benefit by remaining in their natal territory, especially under the scenario of low dispersal costs (Rodrigues & Johnstone 2014). A low dispersal cost favouring natal philopatry in a stable environment seems counter-intuitive but is reasonable because greater numbers of surviving immigrants (outsiders) equalise the intensity of competition between the high- and low-quality patches (Rodrigues & Johnstone 2014). However, if the temporal autocorrelation of resource quality is low – that is, high-quality patches frequently become low-quality patches, and *vice versa* – no consistent RD benefits will accrue to offspring that delay dispersal and CBGs will not form.

Although CA benefits are likely to be more important in fluctuating environments (see below), they can also influence the evolution of sociality in stable environments. For example, in cooperatively breeding pied kingfishers, *Ceryle rudis*, the type of prey and its availability determine the type of grouping benefit available in temporally stable but spatially different Rift Valley lake environments (Reyer 1990). This is because cyprinid fishes, the primary prey in Lake Victoria, have a slender body shape and are nutritionally poorer than cichlid fishes, the primary prey of the same body size in Lake Naivasha. In addition, pied kingfishers spent more time hovering and flying to catch prey in Lake Victoria than in Lake Naivasha because the foraging ground was farther from their colony and strong winds created large surface waves that made prey location more difficult on the larger Lake Victoria. Only 24% of the kingfishers' foraging dives were successful at Lake Victoria, compared with 79% successful dives at Lake Naivasha. As a consequence, the CA benefit of increased provisioning efficiency was consistently more pronounced in the Lake Victoria than in the Lake Naivasha population. Moreover, optimal *per capita* group size at Lake Victoria was always greater than that of a solitary pair, and unrelated joiners were accepted into provisioning CBGs. In contrast, optimal *per capita* group size was not greater than a simple pair at Lake Naivasha, and only close relatives (sons) were accepted into CBGs. These empirical findings are consistent with the different attributes predicted by the dual benefits framework for CBGs that form primarily because of CA or RD benefits, respectively (Table 2).

Dual benefits in temporally fluctuating environments

Environmental fluctuation can influence insider–outsider conflict and its resolution by altering the magnitude of the

grouping benefit, population density or the interaction between the two. In a fluctuating environment, if population density is low following a bad year, insider–outsider conflict over group membership will generally be lower because there will be more breeding vacancies and fewer potential joiners in the population. However, if CA benefits are crucial for breeding success in bad years, insiders could allow more potential joiners – even non-kin – to join the group to obtain increased CA benefits when conditions are poor.

In a temporally variable environment, both environmental conditions and population size can vary among years or other relevant time intervals. When this is the case, the number of lifetime offspring produced is not an appropriate measure of fitness (Grafen 1988; Sæther & Engen 2015) because offspring contribute differentially to future population growth and thus have different reproductive values depending upon whether they are born in a good or a bad year (Fisher 1930; Grafen 2006). As both the absolute value and variation in offspring production jointly determine the long-term genetic contribution of an individual (or more precisely, a genotype), the geometric mean of fitness, G , defined as $(w_1 w_2 w_3 \dots w_t)^{1/t}$, where w_t is the number of offspring at the t -th generation, is a more appropriate measure than the arithmetic mean (Lewontin & Cohen 1969; Gillespie 1973; Cohen 1977; Tuljapurkar & Orzack 1980). However, as it is difficult to directly calculate the geometric mean of fitness for long-lived species like most cooperatively breeding vertebrates, geometric mean fitness is given approximately as $G \approx \bar{w} - \frac{\sigma^2}{2\bar{w}}$, where \bar{w} is the arithmetic mean fitness through time and σ^2 is the variance in fitness through time (Gillespie 1977, 1991; Tuljapurkar 1982; Orr 2009) (see Appendix E for more details). Therefore, arithmetic mean fitness is a special version of a fitness calculation in a stable environment (i.e. $G \approx \bar{w}$ when $\sigma^2 = 0$), where in general, a higher absolute number and lower variance of offspring produced across time steps yield higher geometric mean fitness (Orr 2009). Ultimately, teasing apart the relative importance of environmentally driven mean vs. variance in fitness for cooperative breeders is likely to prove informative for understanding social evolution (Rubenstein 2011).

RESOLVING THE PARADOX OF ENVIRONMENTAL QUALITY AND SOCIALITY WITHIN THE DUAL BENEFITS FRAMEWORK

The distinction between resource defence and collective action benefits helps explain why existing interspecific comparative studies in birds have had difficulty finding a consistent relationship between the incidence of cooperative breeding and ecological or environmental factors (Dow 1980; Brown 1987; Ford *et al.* 1988; DuPlessis *et al.* 1995; Arnold & Owens 1999; Hatchwell & Komdeur 2000; Ekman & Ericson 2006; Rubenstein & Lovette 2007; Jetz & Rubenstein 2011; Gonzalez *et al.* 2013). We suggest that the lack of a clear relationship between social behaviour and climate is largely because cooperative breeding behaviours evolve through two distinctive routes, one based upon CA benefits and the other upon RD benefits.

For example, the ‘life-history hypothesis’ states that low annual mortality rather than any particular feature of breeding ecology is the key factor that predisposes certain avian lineages

to breed cooperatively (Russell 1989; Arnold 1998). Extensions of the life-history hypothesis to incorporate ecology such as the ‘broad constraints hypothesis’ argue that life history predisposes lineages to cooperation but ecological constraints actually facilitate cooperative breeding behaviour (Hatchwell & Komdeur 2000). Both the life-history and broad constraints hypotheses explain the link between life-history traits, habitat saturation and natal philopatry in a stable environment, thus constituting an RD benefit evolutionary route to the formation of CBGs. In contrast, the temporal variability hypothesis argues that unpredictability in highly variable environments favours cooperative breeding as a strategy to either increase mean fitness, especially in poor years, or as a bet-hedging strategy (the ‘bet-hedging hypothesis’) that acts to reduce inter-annual variance in the reproductive success of CBGs (Rubenstein & Lovette 2007; Jetz & Rubenstein 2011). Thus, the temporal variability and bet-hedging hypotheses constitute a CA benefit evolutionary route to the formation of CBGs.

We argue that differentiating between the RD and CA benefit routes for the evolution of cooperative breeding is essential for understanding inconsistent comparative results, as well as for developing a predictive theory for understanding social evolution at the interspecific level. For example, work in African starlings (Sturnidae) showed that cooperatively breeding species are more commonly found in fluctuating environments than non-cooperative species, which suggests that CA benefits could be important for the formation of CBGs in this lineage (Rubenstein & Lovette 2007). However, the reverse pattern was found in hornbills (Bucerotidae), where cooperatively breeding species occur more frequently in stable environments (Gonzalez *et al.* 2013), suggesting that RD benefits could be important for the formation of CBGs in hornbills. Thus, instead of viewing cooperative breeding as a homogeneous phenomenon and simply comparing life-history traits or ecological conditions of cooperative and non-cooperative species, our framework suggests that distinguishing cooperatively breeding lineages in which CBGs initially evolved for RD benefits vs. those where CBGs evolved for CA benefits might provide better resolution in phylogenetic and biogeographic comparative studies.

COOPERATIVE BREEDING IN FLUCTUATING ENVIRONMENTS: A PATH FORWARD

One critical area for future study is to incorporate a more complete theoretical framework of fitness in fluctuating environments that considers fitness effects and demographic implications, and that uses new statistical methods to empirically estimate the fitness of social traits. As a starting point, we know that individuals in CBGs could perform better than solitary breeding individuals in (1) both good and bad years, (2) only good years or (3) only bad years. These three possible scenarios can be explored empirically by carefully quantifying the mean and variance of offspring production with varying local population sizes in good and bad years (Koenig & Walters 2015).

In both good and bad years (scenario 1), long-term genetic contribution will be higher if the absolute number of offspring produced (\bar{w}) is higher under all environmental conditions.

Many obligate cooperatively breeding species fit this scenario, as described earlier in the CA benefit section. Such species represent extreme cases where CA benefits are not only primary, but have also become mandatory, regardless of the environmental conditions. If individuals in CBGs outperform solitary breeding individuals in good years only (scenario 2), the absolute number of offspring produced (\bar{w}) could be higher due to a higher CA benefit in good years, although the variance (σ^2) might also be higher. Although not likely to be common in social species, this situation appears to be the case in acorn woodpeckers *Melanerpes formicivorus*, where helper males contribute significantly to group reproductive success following good, but not poor, acorn years (Koenig *et al.* 2011). Finally, if individuals in CBGs outperform solitary breeding individuals in bad years only (scenario 3), variance in fitness (σ^2) will be lower if CA benefits increase productivity in poor years, but whether the absolute number of offspring produced (\bar{w}) will be higher or lower depends upon the relationship between \bar{w} and σ^2 .

Current hypotheses concerning the evolution of cooperative breeding in fluctuating environments generally emphasise CA benefits in harsh conditions or in fluctuating environments (scenario 3: only bad years, e.g. Emlen 1982; Lehmann *et al.* 2006; Rubenstein 2011; but see Rubenstein & Lovette 2007 for scenario 1). Individuals can gain CA benefits such as cooperative provisioning of young that translate into greater offspring production than solitary breeders in hard times by forming CBGs to cope with harsh environmental conditions but maintain stable groups through different environmental conditions (the 'hard life hypothesis') or by adjusting breeding group size to current environmental conditions (the 'fission–fusion hypothesis') (Emlen 1982; Emlen & Wrege 1991; Rubenstein & Lovette 2007).

Because the hard life and fission–fusion hypotheses describe different mechanisms of increasing offspring production in poor years and thereby reducing overall reproductive variance, it is important to determine the extent to which these processes potentially result in social conflict that may decrease fitness in good years. As described above, if strategies for increasing the mean number of offspring production in poor years have a negative impact on fitness in good years, they can be viewed as bet-hedging strategies. Thus, the CA benefit of enhancing breeding performance in bad years can have the twofold advantage of not only increasing the number of offspring produced over an individual's lifetime (i.e. increasing \bar{w}) but also producing offspring of relatively higher reproductive value by decreasing σ^2 because the difference in productivity between good and bad years will be smaller if relatively more offspring can be produced in bad years (Appendix E).

In summary, if fewer offspring are born in bad years, then the reproductive value of each surviving offspring will be relatively higher than those individuals born in good years (Rubenstein *et al.* 2016). This is because there are fewer cohorts born at the same time, and thus, there is likely to be less competition for breeding resources later in life (Appendix E). This differential reproductive value of offspring also creates the potential for a within-generation bet-hedging strategy by which lower σ^2 and higher \bar{w} result in higher geometric mean fitness, especially in the structured populations such as groups in cooperatively

breeding species (Lehmann & Balloux 2007; Rubenstein 2011). Although within-generation bet-hedging is likely to be rare in nature, it can occur in structured populations like those of cooperative breeders (Gillespie 1991; Lehmann & Balloux 2007; Rubenstein 2011). Testing these ideas will require quantifying the mean and variance of offspring production with varying local population sizes in good and bad years (Koenig & Walters 2015), and thus require measuring a genotype's long-term genetic contribution to the population.

To further understand how environmental fluctuation influences cooperative breeding behaviour, it is also important to measure how local population size – including population levels of fecundity and mortality – vary with environmental conditions. Although lifetime offspring production is not the appropriate measure of fitness in a fluctuating environment if the reproductive value of a given offspring varies among years, statistical methods have been developed to estimate the genetic contributions of different fitness-related social traits such as group size in a fluctuating environment (McGraw & Caswell 1996; Coulson *et al.* 2006; Engen *et al.* 2009; Sæther *et al.* 2016). A crucial next step will be to estimate how population dynamics and environmental conditions jointly influence fitness in cooperatively breeding species.

CONCLUSION

The dual benefits approach provides a predictive theoretical framework for understanding group size, kinship variation and group stability of CBGs in both spatially and temporally variable environments where cooperative vertebrates are more likely to occur (Jetz & Rubenstein 2011; Lukas & Clutton-Brock 2017). It also demonstrates that spatial environmental variation tends to more strongly influence RD benefits, whereas CA benefits are influenced more by temporal environmental variation, thus helping to resolve the paradox of environmental quality and sociality. Ultimately, this framework implicitly proposes two routes for the evolution of cooperative societies: (1) groups in primarily (but not exclusively) spatially variable environments driven by resource defence benefits that are based upon ecological constraints limiting natal dispersal and independent breeding; and (2) groups in primarily (but not exclusively) temporally variable environments driven by collective action benefits that are based upon advantages accrued to individuals because they live together. Perhaps most importantly, the dual benefits framework provides an explanation for the evolution of cooperatively breeding species where individuals benefit directly from group living in the absence of habitat saturation, something that has been the prevailing explanation for cooperative breeding behaviour for more than 50 years (Selander 1964). Finally, by distinguishing among the different ecological bases of social evolution, the dual benefits framework also opens up new directions for studying the ecological consequences of sociality, such as the expansion of niche breadth or range size (Sun *et al.* 2014; Cornwallis *et al.* 2017). Thus, we hope that the dual benefits framework will stimulate further discussion about the role of ecology in the evolution and maintenance of cooperative breeding behaviour, and contribute towards the development of a more general but predictive theory of social evolution.

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AUTHORSHIP

S.-F.S. conceived the idea. All authors contributed to discussion, design and writing of the article.

DATA ACCESSIBILITY STATEMENT

No data.

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