

Commentary

## Integrating delayed dispersal into broader concepts of social group formation

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It is always a challenge to find the right balance between defining a question too narrowly or too broadly. Cooperative breeding has long been the subject of intensive research but has often been studied in relative isolation from other work on sociality, perhaps because the diversity of cooperatively breeding systems has seemed like a broad enough topic to tackle. However, as pointed out by Bergmüller et al. (2007) in this issue, cooperative breeding clearly involves larger concepts, such as cooperation and conflict, and cooperatively breeding systems in turn provide excellent models for investigating such broader issues. They argue that there is much to be gained for both empiricists and theoreticians from finally uniting cooperative breeding research with theoretical work on cooperation. In particular, they propose that helping behaviour in cooperatively breeding species could be better understood if considered in the broader context of general theories to explain cooperative behaviour among unrelated individuals.

We wholeheartedly agree that the time is ripe for broadening the approach to studies of cooperative breeding; however, we believe that a similarly broad approach should also be applied to the issue of delayed dispersal in cooperatively breeding species. Bergmüller et al. (2007) state that “There is a consensus that a key factor explaining why helpers delay dispersal is ecological constraints, which limit the chances to survive or breed independently.” We will argue that they have failed to appreciate the extent to which this consensus has eroded in recent years and that the issue of delayed dispersal is still very much open to debate. Thus, they may not have appreciated the opportunity available to extend their general integrative approach to include delayed dispersal as well as helping behaviour. We suggest that research on delayed dispersal in cooperatively breeding systems

should be integrated with empirical and theoretical work on social group formation in noncooperative systems, and briefly describe one possible framework for accomplishing this task. We believe that, like the approaches proposed by Bergmüller et al. (2007), such integration will yield new insights and identify gaps in our current understanding of cooperative breeding and sociality in general.

### 1. The question of delayed dispersal

As first suggested by Brown (1987), a full understanding of cooperative breeding can only come by answering each of three distinct questions: why delay breeding? why delay dispersal? and why help? In a typical cooperative breeder, at least some individuals engage in all three of these behaviours by becoming nonbreeding helpers on their natal territory, but it is important to note that some individuals and some species can be characterised by any combination of the three. For example, individuals may delay breeding and delay dispersal by remaining in their natal social group but provide no assistance in raising offspring (Ekman et al., 1994; Strickland and Waite, 2001). The three questions represent three independent behavioural decisions, though the costs and benefits of one decision may affect the potential fitness consequences of other decisions. Nonetheless, conceptually separating the question of helping from the other two was a key innovation that helped researchers focus on the specific fitness consequences of helping behaviour, leading to our current understanding of the roles of kin selection and direct benefits in cooperative breeding systems (Cockburn, 1998; Dickinson and Hatchwell, 2004).

Unfortunately, delayed breeding and delayed dispersal were not always consistently treated as distinct behaviours, which led many researchers to prematurely conclude that the question of why individuals engage in these behaviours was answered.

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As alluded to in the statement quoted above from Bergmüller et al. (2007), there was a strong consensus for many years that delayed dispersal was primarily a response to various forms of ecological constraints, most commonly a paucity of suitable mates or territories for breeding. However, as more researchers have taken care to distinguish between the question of delayed breeding and that of delayed dispersal, the consensus on this issue has gradually shifted. Though it had previously been a point made by a minority of authors (e.g., Stacey and Ligon, 1987, 1991; Zack, 1990; Koenig et al., 1992), in recent years it has become more widely acknowledged that even if most cooperatively breeding species are faced with ecological constraints on breeding, so are many if not most noncooperative species (Koenig and Dickinson, 2004). Thus, it has gradually been recognised that while ecological constraints may provide an excellent explanation for delayed breeding in both cooperatively breeding and noncooperative species, they do not adequately explain delayed dispersal (Ekman et al., 2004).

Empirical data have increasingly supported the diminishing importance placed on ecological constraints as a critical factor in determining the occurrence of delayed dispersal (as distinct from delayed breeding). While experimental studies in a few single species have supported a role for constraints (e.g., Komdeur, 1992), the few comparative studies that have simultaneously evaluated ecological constraints in cooperative and noncooperative species or populations have failed to support any key role of such constraints in the evolution of delayed dispersal. Only one study, that of Zack and Ligon (1985) on *Lanius* shrikes, found a correlation between certain ecological constraints and delayed dispersal, while another on Australian treecreepers found no clear correlation (Noske, 1991). However, three different comparative studies have actually found evidence for higher ecological constraints in noncooperative species or populations as compared with their cooperatively breeding counterparts, including studies of Australian thornbills (Bell and Ford, 1986), carrion crows (Baglione et al., 2005), and Australian treecreepers (Doerr and Doerr, 2006). Furthermore, as other research in noncooperative species has shown, individuals that delay breeding due to ecological constraints have a wide variety of options in addition to delaying dispersal, including floating on several breeding territories and joining nonbreeding flocks (Zack and Stutchbury, 1992; Koenig et al., 1992).

Thus, the bulk of available evidence supports the idea that delayed breeding and delayed dispersal are separate behaviours, and although ecological constraints may influence both behaviours, they are not a key determining factor in the evolution or maintenance of delayed dispersal. Rather, ecological constraints are best considered a probable precondition for delayed dispersal, in much the same way that biparental care or altriciality are likely to be preconditions for the evolution of helping behaviour (Ligon and Burt, 2004). While they may create conditions under which the behaviour becomes more likely to evolve, they generally have little predictive power. As a result, the phenomenon of delayed dispersal is once again in need of a definitive explanation.

## 2. Delayed dispersal as social group formation

Probably because they take the “why delay dispersal?” question as answered, Bergmüller et al. (2007) devote all their attention to the “why help?” question, but we believe both questions are amenable to their integrative approach. Interestingly, they define cooperation as “an interaction between two or more individuals” and cooperative behaviour as “an action or actions taken by a single individual” (Bergmüller et al., 2007). Therefore, by considering the question of “why delay dispersal?” in a broader theoretical context, we can attempt to explain cooperation (i.e. the formation of social groups via delayed dispersal) and not just cooperative behaviour (i.e. helping behaviour). We suggest that the best way forward is to consider cooperative breeding as just one type of group breeding and bring to bear on the issue all of the vast body of theoretical and empirical work on the topic of group living.

Just as helping behaviour in cooperatively breeding species has often been studied separately from general theories of cooperation, group formation in cooperatively breeding species has traditionally been considered a unique process. Few parallels have been drawn between delayed dispersal and the decision to join other types of social groups, such as a colony or a polygynous group. However, delayed dispersers are at the most basic level choosing to join social groups with breeding individuals, just as individuals who join colonies or polygynous groups do. We do not mean to suggest that there are no unique aspects to delayed dispersal—merely that new potential explanations for the behaviour might productively be sought by recognising this basic similarity and considering the broader literature on social group formation.

## 3. A new framework for the study of group breeding

We have been working with Paul Sherman and David Winkler to develop a novel theoretical framework that brings together individual and population-level approaches to understand the reasons why individuals choose to join breeding groups (Safran et al., in press). Essentially our framework attempts to identify the individual-based decision rules that drive the formation and maintenance of various types of breeding groups (including colonies, polygamous groups, and even cooperatively breeding groups). Recognising that the most common denominator among socially breeding organisms is some kind of habitat-selection process which may or may not be influenced by the conspecifics that are already inhabiting a given space, we propose that the site-selection decisions of group breeders should be analysed to determine the relative importance of habitat-based resources versus conspecific-based resources as clues to determining the underlying cause of group breeding. In other words, we can best understand social systems and why they are formed and maintained by answering the question: are the habitat-selection decisions of individuals principally governed by the intrinsic characteristics of a particular site or by the characteristics of individuals already present on that site? Once such habitat-selection cues are identified, fitness consequences can be verified to show that group joining decisions are adaptive

and individual behaviours can be used collectively to predict population-level patterns of variation in group breeding (e.g., distributions of group sizes; Safran, 2004). Although both types of factors can operate simultaneously, we assert that, in most populations and most species, group formation will be driven primarily by either conspecific-based resources, termed social benefits, or by habitat-based resource patchiness. We further provide a number of guidelines that allow researchers to quickly distinguish between social groups formed for these two different reasons.

While this conceptual framework for studying group breeding does not deal with cooperative breeding in great detail, we believe that cooperative breeding systems can and should be considered within this broader group-breeding framework. One could argue that individuals that delay dispersal are not “joining” a group, but rather remaining in a group, but we feel this would be semantic quibbling. The crucial thing is that an individual must make the decision between living solitary, as a member of a pair, or as part of a larger group. Whether the individual in question is from a cooperatively breeding species, a colonial species, or a polygynous species, we would suggest that the same types of constraints, benefits, and costs are likely to influence the decision to live in a group or not.

By focusing on resource patchiness and social benefits as the primary drivers of group formation, including group formation via delayed dispersal, we can construct a hierarchical classification of mechanisms that may cause different types of social groups to form, similar to Bergmüller et al.’s (2007) hierarchical classification of mechanisms to maintain cooperative behaviour (Fig. 1). Simply by taking this first step to apply broader theories of social group formation to the issue of delayed dispersal, we can already derive a few key insights. First, it is immediately apparent that similar ecological pathways can lead to cooperative breeding or to other types of social groups (colonial or polygynous groups), the key determinant being the decision to breed or not. However, it is worth noting that polygyny (or polyandry or polygynandry) can occur within many cooperatively breeding species that may or may not also have nonbreeding helpers. Thus, this hierarchy conceptually unites ecological routes to several different forms of cooperative breeding. Second, Fig. 1 also reveals that there are multiple pathways to delayed dispersal, so a single ecological explanation for the behaviour may prove elusive. Finally, it is significant that cooperative breeding allows for an iterative decision-making process in which individuals delaying dispersal may continually reassess the level of ecological constraint on breeding and make different decisions. Greater recognition of the commonalities between different types of breeding groups and the different combinations of factors that can produce them should lead to new advances in our understanding of cooperative breeding and sociality in general.

We agree with Bergmüller et al.’s (2007) proposition that advances in understanding of helping behaviour will be facilitated by integrating cooperative breeding research and general theories of cooperation. We further challenge researchers to simultaneously work towards better understanding of the formation of cooperatively breeding groups via delayed dispersal

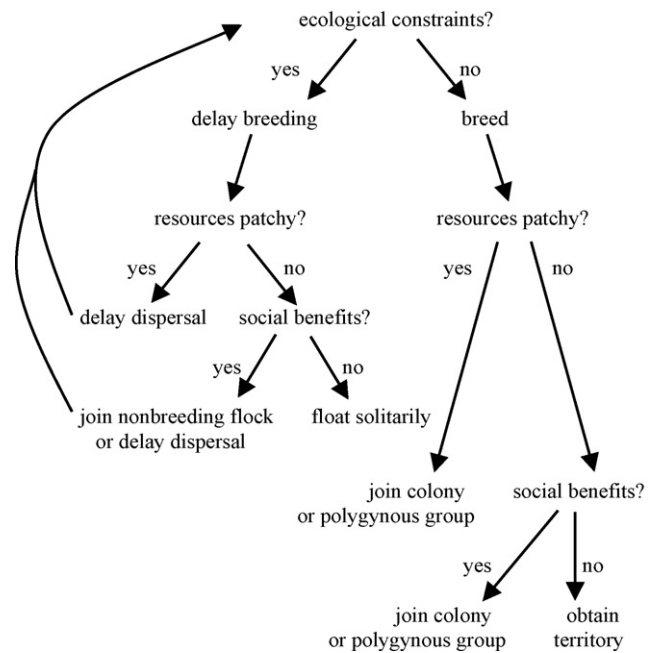


Fig. 1. Hierarchical classification of mechanisms that can cause different types of social groups to form. When a hierarchy of decisions ends in delayed dispersal, a cooperatively breeding group may form. When a series of decisions ends in joining a colony or a polygynous group, a breeding group forms. When decisions end in obtaining a territory or floating solitary, no social group is formed beyond a simple pair bond. Note that individuals that delay dispersal reassess the degree of ecological constraints again in the future and may make a different series of decisions.

by integrating cooperative breeding research and more general theories of group formation and group breeding.

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