

Group breeding in vertebrates: linking individual- and population-level approaches

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ABSTRACT

Background: Why individuals breed in groups and why patterns of group breeding are so variable are long-standing questions in evolutionary ecology. Researchers have tended to study either population-level patterns such as breeding group size or else the decisions that individuals make when joining groups, but have rarely explicitly linked the two, using knowledge of individual decisions to predict larger-scale population patterns.

Aim: We describe an integrated method designed to categorize and explain a diversity of vertebrate social systems, with a focus on colonial breeding. This approach places group breeding within an evolutionary context by first elucidating the process of group formation, identifying decision rules that individuals use when joining groups, and verifying their fitness consequences, then using these individual-level processes to predict and understand patterns of population-level variation.

Results: To facilitate the identification of decision rules, we differentiate between groups that form as a consequence of resource patchiness, and groups that form because individuals derive social benefits from breeding in close association with conspecifics. We next demonstrate how these decision rules inform us about the maintenance of population-level patterns of group breeding, like group size variation.

Worked examples: We illustrate this process-to-pattern approach with several empirical examples, highlighting its efficiency relative to the more traditional approach of defining pattern first. By identifying individual-based decision rules in four different vertebrate taxa, we demonstrate the power and utility of using individual-level decision making to explain larger-scale patterns of group living.

Keywords: coloniality, group breeding, group size, individual decisions, resource patchiness, social benefits, sociality.

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INTRODUCTION

Group breeding occurs whenever individuals reproduce in close proximity to adult conspecifics. Why individuals breed in groups is a long-standing question in ecology and evolutionary biology because there is fascinating yet unexplained variation within and among groups in the costs and benefits incurred by a given individual. For example, one benefit of group breeding is the proximity to reproducing conspecifics, which may afford extra-pair fertilization opportunities (e.g. Morton *et al.*, 1990; Westneat and Sherman, 1997; Neff *et al.*, 2004), but which comes at an obvious cost to pair-bonded individuals within the group. Coloniality is a predominant form of group breeding among vertebrates, especially birds, and is perhaps the clearest example of the phenomenon, as all group members are independent breeders and thus face similar decisions about joining a given colony (Brown and Brown, 2001; Krause and Ruxton, 2002). Despite extensive long-term studies of colonial species (e.g. Brown and Brown, 1996), recent reviews have pointed out that much of the variation among colonies, particularly variation in breeding group size, still remains unexplained (e.g. Brown *et al.*, 1990; Brown and Brown, 2001). Thus, despite extensive research, questions remain about both individual decisions and population patterns in group-breeding systems.

In this paper, we suggest that the most effective way to address remaining questions about group breeding and coloniality in particular is to combine individual-level and population-level research approaches and explicitly make connections between individual decision making and variability in group or population traits. Many studies have focused on either individual decisions or population patterns, and each of these levels of organization has provided great insights into the evolution and ecology of group breeding. However, there is additional progress to be made by linking the two to understand how processes at the individual level generate patterns at the population level. In addition to identifying the settlement cues individuals use when deciding to join groups, such studies also need to establish the adaptive significance of these choices, and thus take advantage of the powerful framework of evolutionary ecology. Most importantly, once decision rules have been identified, they should be used to predict population-level patterns of variation in group breeding, including distributions of group sizes, group composition, and group or population densities. Here, we describe this kind of integrated approach, designed to evaluate the group formation process from an individual perspective and to use individual decision rules to predict patterns of variation in group breeding within and among populations. We suggest that most population-level patterns, such as group size variation in colonial breeders, will be predictable once the underlying decision-making process and the distribution of cues in the environment are identified. Thus, using process to predict pattern provides an efficient way to derive new insights related to group breeding.

CURRENT APPROACHES TO STUDYING GROUP BREEDING

Many studies of group breeding in vertebrates have examined the fitness consequences of population- or group-level characteristics, usually by calculating average reproductive success or survival in groups of different sizes (Hoogland and Sherman, 1976; Snapp, 1976; Krebs and Davies, 1981; Møller, 1987; Brown *et al.*, 1990; Brown and Brown, 1996, 2001). For example, many studies have attempted to quantify the optimal colony size in a population, the group size that confers the greatest fitness payoffs, on average, to individuals at the site (Brunton, 1999; Arroyo *et al.*, 2001; reviewed in Brown and Brown, 2001; Weaver and Brown, 2005). Once the optimal colony size is identified,

we expect that it will explain the distribution of group sizes in the population, which should be narrow and centred on the optimum. However, in many cases, the observed range of group sizes is much broader than the predicted distribution (Sibley, 1983). For example, Brown and Brown (1996) determined that small to intermediate group sizes are optimal for cliff swallows (*Petrochelidon pyrrhonota*) in terms of the net benefits associated with groups of different sizes, and yet group sizes were still highly variable, ranging from one to several thousand breeding pairs. Similarly, in lesser kestrels (*Falco naumanni*), reproductive success increases with group size, but individuals still breed solitarily as well as breeding in groups of up to 100 pairs (Serrano *et al.*, 2001). Thus, assessing average fitness payoffs for groups of different sizes is frequently not sufficient to understand why individuals choose to join groups of different sizes

As an alternative, an individual-level approach has been used to investigate group-joining decisions in colonial species. For example, Shields *et al.* (1988) suggested that, to understand colony-size distributions (in barn swallows), it would be valuable to identify the general cues that individuals use when selecting colony sites. Perhaps the most important contribution to the study of individual settlement decisions, both for group formation and habitat selection, has been the development of the conspecific attraction hypothesis (Reed and Oring, 1992; Cadiou *et al.*, 1994; Boulinier and Danchin, 1997; Danchin *et al.*, 1998). The idea is that individuals use the presence of conspecifics or, if available, information about the prior reproductive success of conspecifics as cues in making settlement choices. Danchin and Wagner (1997) highlighted the conspecific attraction hypothesis as an explanation for colony formation in birds and emphasized its focus on individual decisions. In addition, at a mechanistic level of analysis, Brown *et al.* (1990) proposed that individuals have heritable differences in colony size preferences and that heritability of a group-size selection template could explain the diversity of colony selection decisions among individuals (Brown and Brown, 2000).

However, studies that focused on the individual as the unit of analysis when understanding settlement and group formation cues have rarely also assessed the fitness costs and benefits of those decision rules. For example, the conspecific attraction hypothesis itself does not explain how individuals might benefit from settling near conspecifics; therefore, it does not make predictions about why individuals should settle in particular groups, what the distribution of group sizes should be in the population, or even why individuals should breed in groups at all. In fact, conspecific presence or reproductive success may simply indicate higher quality habitat, and some of the best empirical evidence in support of the hypothesis comes from research on pair-territorial rather than group-breeding species (Doligez *et al.*, 2002, 2004). Thus, just as for population-level approaches, identifying cues used by individuals during settlement and group formation may not be sufficient to explain larger-scale patterns, such as the range of variation in group sizes.

To provide new insights, we suggest that individual- and population-level research on group breeding should be united by identifying the cues that individuals use to make site-selection decisions and also evaluating the costs and benefits of those decisions. These are complementary approaches, both of which are needed to evaluate the proximate and ultimate reasons why individuals choose to join particular groups. Furthermore, such a detailed understanding of the group-formation process at the individual level should then be verified by using it to predict population-level patterns in sociality. The economic framework of previous population-level pattern-based studies (e.g. weighing the costs and benefits of group living across different group sizes) has sometimes been criticized (Danchin and Wagner, 1997). However, we believe that the economic approach applied at the *individual*

level can help to verify selection for particular individual decision rules. In habitat selection studies, there is increasing recognition that both differential settlement patterns and fitness consequences of those individual choices must be demonstrated (Martin, 1998; Clark and Shutler, 1999; Jones, 2001; Doerr *et al.*, 2006). The same principles should apply to studies of social group formation.

AN INTEGRATED INDIVIDUAL-BASED APPROACH

To link individual- and population-based research on group breeding and thus explain decisions and patterns at both levels, we developed an integrated individual-based approach that involves three steps: (1) determine, at the outset, the primary cues individuals use when selecting sites or groups to join; (2) evaluate whether decisions based on these cues have predictable fitness consequences for individuals; and (3) determine whether group-level patterns (e.g. group size variation, density of breeding groups) result from this decision-making process.

Identifying cues and decision rules

Potential settlement or group-joining cues include not only the presence or reproductive success of conspecifics (though they have been most widely studied in colonial species), but also conspecific behaviour and habitat- or resource-related cues. Testing for the use of all possible cues in any given group-breeding system would be an enormous task and would thus eliminate much of the advantage of using a process-to-pattern approach. However, individuals in group-breeding species should use which ever cues provide the most reliable information about expected fitness, regardless of whether they are conspecific- or resource-based. Thus, preliminary investigations into the type of fitness benefits associated with any given group-breeding system should suggest a smaller subset of cues that warrant further investigation.

Starting with Alexander (1974), benefits related to access to resources or to social interactions have been considered as contrasting explanations of the causes of colonial breeding (reviewed in Brown and Brown, 2001; Krause and Ruxton, 2002). Most breeding colonies are unevenly distributed across a landscape, and the principal environmental feature that can constrain or facilitate colonial breeding is spatial patchiness in environmental resources (resource patchiness). Alternatively, individuals may choose to breed near others because they obtain benefits from such associations (social benefits). Social systems that arise primarily as a consequence of these social benefits (SB) can be inherently different from those that arise due to resource patchiness (RP). Although the costs of colonial breeding apply to individuals in both situations [e.g. competition and disease transmission (Alexander, 1974)], the benefits of RP and SB group breeding differ dramatically. Resource patchiness species do not gain benefits associated with breeding near conspecifics. Instead, colonial breeding is an incidental effect of the availability, density, and patchiness (or spatial variance) in the quality of resources. By contrast, in SB species, individuals benefit from breeding in close association with conspecifics. Thus, one system (SB) is maintained because of benefits associated with the presence of conspecifics, whereas the other (RP) is maintained solely as a consequence of resource distributions. As a result, there are fundamental differences between these groups, including the behaviour of individuals within them, the benefits individuals receive from group breeding, and the cues they use to make settlement decisions.

The most efficient way to determine the primary cues that individuals use when deciding to join a breeding colony is therefore to begin by considering whether resource patchiness or social benefits are primarily responsible for maintaining group breeding. Critical predictions of these models and characteristics of RP and SB groups are listed in Table 1, which can be used as a checklist to determine which category *best* describes a given system. Populations may be appropriately classified as either RP or SB based on which type is supported by a majority of the group and individual-level criteria outlined in Table 1. The criteria should be relatively easy to assess, as they are based on relationships between factors such as reproductive success and group density, physical position within the group, and nearest-neighbour distance, which could all be quantified during a single breeding season.

Theoretically, both resource patchiness and social benefits could be in operation (Fig. 1). For example, it is interesting to consider that RP groups may set the stage for the evolution of SB groups (Armitage, 2007; Hare and Murie, 2007). If a species or population is currently in that evolutionary transition, it may be difficult to classify. However, it is likely rare that a given population would be completely balanced between the two, so one process should predominate. This is analogous to the study of male secondary sexual characteristics, which may be maintained by both male–male competition and female choice (Tarof *et al.*, 2005; Griggio *et al.*, 2007), although one process tends to be more important in any contemporary population. The classification of breeding groups as RP or SB groups as a first step also ensures that researchers examine both possibilities empirically, and it is an efficient way to suggest likely hypotheses about the primary cues that individuals use when deciding whether or not to join groups. Examples of applying these criteria to a range of species and using them to infer potential group-joining cues are also presented in Table 1. Hypotheses about the settlement

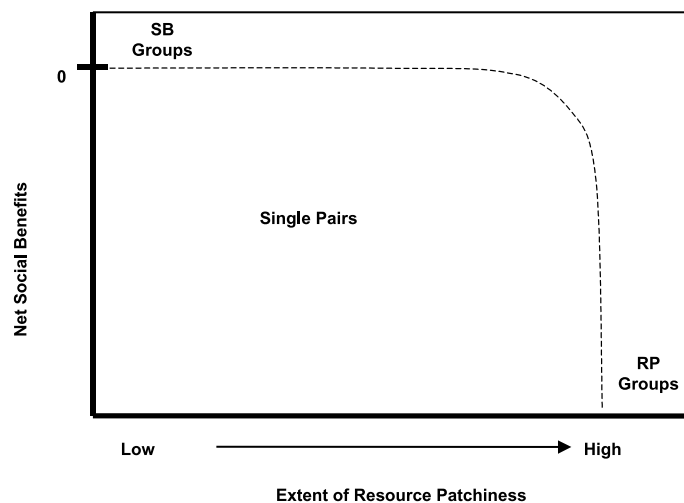


Fig. 1. Solitary or pair living, the predominant breeding system in vertebrates, is expected when *both* resource patchiness (RP) and social benefits (SB) are relatively low. The dashed line portrays a threshold beyond which group breeding results as a consequence of either or both being relatively high. While social benefits and resource patchiness are not mutually exclusive influences, in practice, one factor or the other will be predominantly responsible for the maintenance of group breeding in most species.

Table 1. Criteria for classifying species as RP or SB depending on whether groups form due to resource patchiness (RP) or social benefits (SB), and the settlement and thus group formation cues that individuals are most likely to use based on this classification

Resource patchiness	Social benefits	Bank swallow, <i>Riparia riparia</i>	Barn swallow, <i>Hirundo rustica</i>	Cliff swallow, <i>Petrochelidon pyrrhonota</i>	Clown anemonefish, <i>Amphiprion percula</i>	Meerkat, <i>Surricata suricatta</i>	Southern elephant seal, <i>Mirounga leonina</i>	Red-cockaded woodpecker, <i>Picoides borealis</i>
Type of breeding group:								
Groups are associated with the presence of key resources and so group size may reflect the distribution of those resources	Group sizes depend more on conspecifics, not on the distribution of key resources alone	SB (Hoogland and Sherman, 1976)	RP (Safran, 2004)	SB (Brown and Brown, 1996)	SB (Buston, 2003b)	SB (Clutton-Brock <i>et al.</i> , 1999a, 1999b)	RP (McCann, 1980)	RP (Carrie <i>et al.</i> , 1998)
No relationship or a negative relationship between reproductive success and/or survival and group size	A positive relationship between reproductive success and/or survival and group size because specific benefits increase with group size, although they may asymptote or decline at the largest group sizes	SB (Emlen and Demong, 1975; Hoogland and Sherman, 1976)	RP (Snapp, 1976; Shields and Crook, 1987; Safran, 2004)	SB (Brown and Brown, 1996)	RP (Buston, 2004a)	SB (Clutton-Brock <i>et al.</i> , 1999a, 2001a; Russell <i>et al.</i> , 2002)	U	RP (Walters, 1990; Walters <i>et al.</i> , 1992)
Group density is negatively correlated or shows no relationship with reproductive success and/or survival	Group density is positively correlated with reproductive success and/or survival	SB (Hoogland and Sherman, 1976)	RP (Brown and Brown, 1996)	Mixed (Brown and Brown, 1996)	RP (Buston, 2004a)	SB (Clutton-Brock <i>et al.</i> , 1999a)	RP (Baldi <i>et al.</i> , 1996)	RP (Conner <i>et al.</i> , 1999)

Solitary or single pair options are chosen first, or in no particular order	U	RP (Safran, 2004)	U	RP (Buston, 2003a, 2004b)	U	N/A	RP for females (Walters <i>et al.</i> , 1992) SB for males (Pasinelli and Walters, 2002)
Individuals maximize nearest-neighbour distance	SB (Hoogland and Sherman, 1976)	RP (Brown and Brown, 1996)	SB (Brown and Brown, 1996)	N/A	SB	RP (Baldi <i>et al.</i> , 1996)	N/A
Individuals do not prefer the centre of groups and may prefer the edges. Settling in the centre, or the proportion of time spent in the centre, is not associated with or is negatively associated with fitness	SB (Hoogland and Sherman, 1976)	RP (R.J. Safran, unpublished data)	SB (Brown and Brown, 1996)	N/A	SB (Clutton-Brock <i>et al.</i> , 1998)	U	N/A
Timing of breeding depends only on environmental conditions, not on the behaviour of conspecifics	U	RP (R.J. Safran, unpublished data)	SB (Brown and Brown, 1996)	N/A	SB (Clutton-Brock <i>et al.</i> , 1999b; O'Riain <i>et al.</i> , 2000; Russell <i>et al.</i> , 2003)	RP (McCann, 1980; Lewis <i>et al.</i> , 2004)	U

(continued)

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Resource patchiness	Social benefits	Bank swallow, <i>Riparia riparia</i>	Barn swallow, <i>Hirundo rustica</i>	Cliff swallow, <i>Petrochelidon pyrrhonota</i>	Clown anemonefish, <i>Amphiprion percula</i>	Meerkat, <i>Suricata suricatta</i>	Southern elephant seal, <i>Mirounga leonina</i>	Red-cockaded woodpecker, <i>Picooides borealis</i>
Type of breeding group:								
None of the behaviours listed in the next cell are performed by multiple individuals in a coordinated manner	One or more of the following are performed by multiple individuals in a coordinated manner: anti-predator behaviours, hunting/foraging, provisioning young	Colonial SB (Hoogland and Sherman, 1976)	Colonial RP (Snapp, 1976; Shields, 1984; Møller, 1987; Shields <i>et al.</i> , 1988)	Colonial SB (Brown, 1986, 1988a, 1988b; Brown and Brown, 1987)	Cooperative RP (Buston, 2004a)	Cooperative SB (Clutton-Brock <i>et al.</i> , 1999c, 2000, 2001b)	Polygynous RP (Field <i>et al.</i> , 2001)	Cooperative RP (Hooper and Lennartz, 1981)
Classification								
Potential settlement cues		SB conspicuous number, conspecifics at same nesting stage, conspecific behaviour	RP nesting sites, nesting substrate, re-usable older nests	SB conspicuous number, conspecifics at same nesting stage, conspecific behaviour	RP anemone presence, anemone size, lack of conspecific competitors	SB conspicuous number, conspecific density	RP nesting beaches, offshore foraging areas	RP cavities for nesting and roosting, food resources

Note: Examples are provided using swallows, a particularly well-studied taxonomic group, and representatives from other taxonomic groups. U = data not available. N/A = not applicable to species.

cues used can then be tested by studying individuals and the group-joining choices they make. We therefore offer this dichotomous classification not as a complete theory for the evolution of group breeding, but as a methodological *starting point* for understanding the maintenance of group breeding in any given population.

Constraints on choice

Despite the advantages of the RP/SB classification as a first step in determining the group-joining decisions that individuals use, RP and SB models implicitly assume that individuals have perfect knowledge of all settlement options and complete freedom of choice. These are common assumptions in most models of settlement choice, including the classic ideal free distribution models (Fretwell and Lucas, 1969), but these assumptions are probably violated in most animals in nature. Certainly for both RP and SB species, individuals are time and energy limited in their ability to sample the environment and acquire information about all possible settlement options (Reed *et al.*, 1999). There may also be social constraints on choice as the status of competitors or behaviour of existing group members may influence settlement options (e.g. Rendón *et al.*, 2001; Ekman and Griesser, 2002; Buston, 2003a; Serrano and Tella, 2007).

In strongly hierarchical groups, or groups where individuals settle asynchronously, the RP/SB classification is still useful, but it should be kept in mind that dominant or early-arriving individuals have the greatest freedom of choice, whereas the decision rules of subordinate or late-arriving individuals may be more constrained. In such cases, an investigation of multiple classes of individuals (e.g. first-time breeders and experienced breeders, dominants and subordinates, existing group members and group joiners) may be required to understand social system dynamics. For example, in lesser kestrels, social interactions strictly limit the settlement options of younger individuals, while older birds are free to settle at the best sites and conform to the criteria identified in Table 1 (Serrano *et al.*, 2004).

When individual choices are limited by imperfect knowledge of settlement options, group-formation decisions will be easiest to identify by observing individuals throughout the dispersal and settlement process to compare groups that individuals choose to settle in with those actually sampled, but not chosen, by the same individuals. Although this approach may not always be possible, new methods and technologies that increase its feasibility are continually emerging (Doerr and Doerr, 2005). Even when search abilities are severely limited, individuals should still choose the best group-breeding option from the subset of options they are aware of, using settlement cues that reflect the benefits they obtain from group breeding.

Fitness consequences and population patterns

By formalizing the distinctions between RP and SB groups, we can determine whether the cues individuals use when deciding to join groups are likely to be primarily based on resources or conspecifics. We can then determine whether specific cues are actually used by potential settlers, even when there are constraints on the ability to search for or freely choose a group to settle in. Once these cues and decision rules are identified, it should be straightforward to verify that they have predictable fitness consequences, and thus that individual decision rules are under natural selection. Finally, we can determine whether the combination of adaptive individual decisions and the distributions of conspecific and

resource cues in the environment explain observed population-level patterns of variation in group breeding.

When groups are maintained by resource patchiness, individuals should primarily use features of the environment to make settlement decisions, although the current or past presence of conspecifics can indicate that resources are likely to be available at a particular site (Shields *et al.*, 1988; Safran, 2004). Thus, group-level characteristics, such as distributions of groups, group sizes, and densities should be predictable based on the distribution of resource-related cues. By contrast, SB breeders consider conspecifics to be the valuable resource, and are willing to forego some access to environmental resources to breed closer together. Rather than cueing solely on resource densities, individuals cue on conspecifics, as well as additional characteristics of the biotic environment. These cues may include the presence or density of conspecifics, conspecific behaviour as an indicator of their quality as potential cooperators, the density of predators (and thus potential benefits of group defence), and the presence of food items that require cooperation for efficient exploitation. Thus, group-level characteristics may not be as easy to predict in SB breeders because they can depend on an interaction between multiple factors rather than simply the distributions of either simply resources or conspecifics.

EXTENDING THE APPROACH TO OTHER BREEDING GROUPS

When developing our integrated approach, we focused on coloniality as the most common form of group breeding, in which all individuals are independent breeders. However, there are other forms of group breeding, including cooperative breeding (aggregates of breeding individuals and their helpers) and polygamy (aggregates of breeders where a male or female shares a mate with another same-sex breeder), in which all individuals may not have the same breeding status. Nonetheless, all these systems involve individuals making decisions about whether or not to join or remain in a group during the breeding season (Doerr *et al.*, 2007), so the integrated individual-based approach may still be a useful technique for generating new insights. Although the evolutionary and ecological contexts in which these groups form may differ dramatically, in practice the decision rules leading to the formation of colonial, cooperatively breeding, and polygamous groups all centre on issues such as the quality of potential mates or conspecifics in the group, ecological variables including predation risk and food availability, and the possibilities for direct and kin-related benefits.

Greater reproductive asymmetries may occur within cooperative or polygamous groups, including those between breeders and non-breeders, and between primary and secondary breeders. These asymmetries might mean that different types of individuals use different settlement cues, although this does not differ greatly from situations in colonial systems in which subordinate individuals may be more constrained in their choices than dominant individuals. In addition, some types of individuals (particularly non-breeders) may have to use a suite of criteria when deciding whether to join a group, including the quality of potential mates or refugia from predators in addition to the predicted benefits of being in the group *per se*. Thus, predicting population patterns may require some knowledge of how multiple decision rules interact. However, the integrated approach can help researchers recognize these asymmetries and begin to identify the sets of cues and decision rules that apply to different types of group members.

Benefits of extending the approach: the sociality threshold model

To illustrate further the conceptual advances that can be gained by emphasizing the similarities rather than the differences between all types of group breeding, we have developed a general sociality threshold model. Variance in territory or site quality has previously been implicated in the evolution and maintenance of sociality (Snapp, 1976; Shields *et al.*, 1988; Stacey and Ligon, 1991). This concept has been applied separately to polygynously breeding groups by Orians (1969) in his polygyny threshold (PT) model, to cooperatively breeding groups by Koenig *et al.* (1992) in their delayed dispersal threshold model, and to habitat selection in general by Fretwell and Lucas (1969) in their ideal free distribution (IFD) model. By recognizing the common structure of these models and their applicability to colonial groups as well, we can generate the basic sociality threshold model depicted in Fig. 2.

The polygyny threshold model and the IFD model both consider individual fitness as a function of two variables: (1) the number of individuals in a patch (IFD) or territory (PT), and (2) the intrinsic quality of the patch or territory. In both models, the decisions that individuals make about where to settle provide feedback to the system in that one individual's choice changes the relative payoffs of different patches (or territories) for future patch selectors. Figure 2 is a graphical model with these elements; we use this graphical model to focus on optimal decision rules that would govern whether an individual chooses a solitary site or one with a certain number of conspecifics in close proximity. This is analogous to the choice considered by Orians (1969) in the polygyny threshold model (i.e. should an individual female settle with an unpaired male or one that already has a mate?) and is similar to the choice depicted in the delayed dispersal threshold model (Koenig *et al.*, 1992) between floating solitarily or delaying dispersal and thus choosing to live in a group. We depict the graphical model in two dimensions as a plot of fitness versus habitat quality, with the effects of different numbers of conspecifics shown by different lines. Note that the model could just as easily be depicted like the IFD model: fitness versus consumer number, with patches of different intrinsic qualities shown by different lines. We have chosen to depict it as we do to facilitate examination of threshold values in patch quality.

In the examples that follow, we assume that a focal individual must choose between patch #1, which is unoccupied, and patch #2, which has conspecifics in it. We ask the questions: Should the individual settle solitarily or join the group, and how do relative patch qualities influence the optimal decision? Let $F(q_i, n_i)$ represent the fitness a focal individual would have in patch i , given that patch i is of quality q_i and has n_i other conspecifics in it. Let k_i represent the particular number of conspecifics in patch i at the time the focal individual is making its decision. We define $k_i = k_0 = 0$ if patch i is unoccupied. Consider first a species in which conspecifics gain no benefits from breeding in proximity to each other (Fig. 2a), i.e. an RP species. In a patch of a given quality, q_i , a solitary individual would always have higher expected fitness than $k_i (> 0)$ individuals in a group in the same quality patch, because the solitary individual (by definition) has no competitors for the resources [Fig. 2a; $F(q_i, 0) - F(q_i, k_i) > 0$]. However, suppose that while patch #2 is occupied ($n_2 = k_2 > 0$), it is also of higher quality ($q_1 < q_2$). Should the focal individual choose to breed as an isolated pair in the poorer quality patch or join the group in the higher quality patch? If the focal individual behaves optimally, then it should choose to join the group only if q_2 is sufficiently greater than q_1 , i.e. if $q_2 - q_1 > \Delta q^*$, where Δq^* represents a 'sociality threshold'. The sociality threshold (analogous to the polygyny threshold and the delayed dispersal threshold) can be defined as the difference in patch qualities necessary to offset the costs of joining

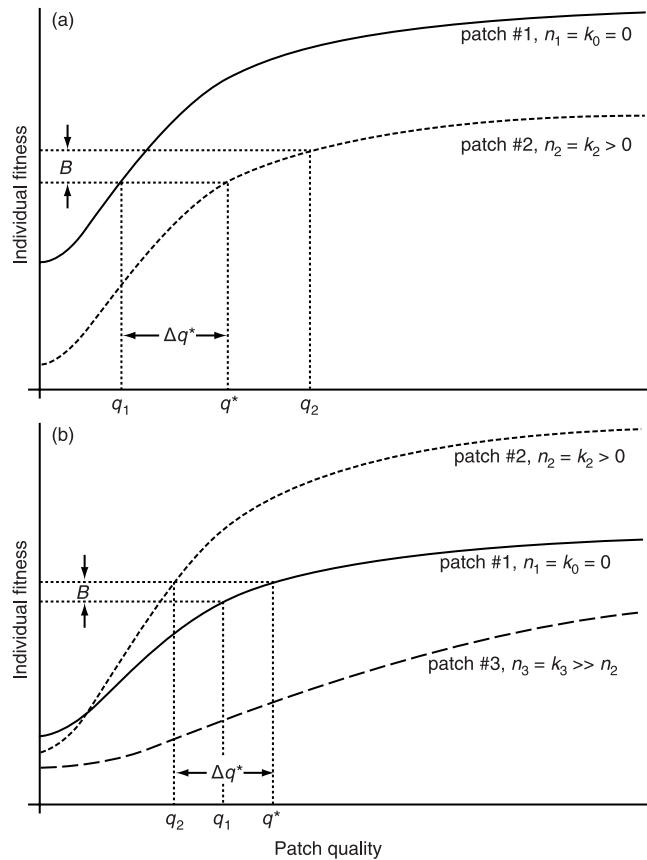


Fig. 2. The sociality threshold model. In all cases, the expected fitness of an individual increases with patch quality. In both panels, the solid line represents the expected fitness of a focal individual if it chooses an unoccupied patch, denoted #1 (see text for more details). The short-dashed line is the expected fitness of the focal individual if it joins the group of size $n_2 = k_2$ in patch #2. The long-dashed line in panel (b) shows the individual's fitness if it joins a very large group of size $n_3 = k_3$ in patch #3. (a) If groups form due to resource patchiness (RP), individuals incur a fitness cost for joining a group relative to remaining solitary in the same quality patch (the dashed line is always below the solid line). However, a net fitness benefit of group breeding (B) can still be gained by joining a group if the patch containing the group is sufficiently higher in quality than available solitary habitat, as is the case in this example ($q_2 \geq q^* > q_1$). The sociality threshold ($\Delta q^* = q^* - q_1$) represents the difference in patch quality at which the fitness of the individual would be the same regardless of whether it joined the group in patch #2 or was solitary. (b) When groups form due to social benefits (SB), individuals gain a fitness benefit for joining a group relative to being solitary in a patch of the same quality. Now the sociality threshold, $\Delta q^* (= q^* - q_2)$, represents the amount by which the quality, q_1 , of an unoccupied territory ($n_3 = k_0 = 0$) must exceed the quality, q_2 , of one with $k_2 (> 0)$ individuals for an individual to choose to be solitary. In the example shown, $q_1 > q_2$, but the difference in qualities does not exceed the sociality threshold. Social benefits more than make up for the difference and the individual should join patch #2. In patches of extremely poor quality (left end of the figure) or in groups of extremely large size (k_3), the benefits of conspecifics are reduced relative to the costs, and solitary individuals may have higher fitness than individuals in groups.

a group relative to breeding solitarily. The minimum value of patch quality that would meet this requirement, q^* , is shown as an example (Fig. 2a). In this example, the difference in patch qualities exceeds the sociality threshold ($q_2 > q^*$), and thus – relative to being solitary – the individual gains an overall benefit B from joining the group [i.e. $F(q_2, k_2) - F(q_1, 0) = B > 0$] in spite of the costs of group membership.

In SB species (Fig. 2b), we expect that the positions of the curves will be nearly the reverse of that shown in Fig. 2a. (Note that a situation like Fig. 2b was not considered in the original polygyny threshold model.) In SB species, joining the group would usually be favoured over solitary breeding for two patches of the same quality. Exceptions could occur in two (extreme) circumstances. First, if available patches are of very poor quality (e.g. due to temporal environmental variation), costs of competition for severely limited resources might outweigh social benefits. This is shown in the graphical model at the extreme left of Fig. 2b, where the dashed line (fitness if in a group) is below the solid line (fitness if solitary). Second, as groups become larger, social benefits may accrue with diminishing returns while costs continue to escalate. This is reflected in Fig. 2b in the position of a curve shown for a third patch (patch #3) with $k_3 \gg k_2$. If effects of the latter type occur, they will place some upper limit on the size that groups will reach [just as in Fretwell and Lucas's (1969) 'Allee-type' IFD]. Fitness decrements in these extreme cases provide feedback to the system that prevents the population from forming one huge group in the first-settled patch. Such feedbacks may not exist in all SB species, but we expect that – based on well-known, taxonomically broad patterns of social costs and benefits – these feedbacks are likely to apply to most species. However, our assumption of their existence does not change the major predictions of our model.

In addition to these extreme cases, solitary individuals are expected to breed in sites that exceed the quality of available group sites by the sociality threshold. Furthermore – unless vacant, high-quality patches occur frequently – solitary breeding at such sites should be temporary, as it would benefit future settlers and individuals from lower quality patches to join the currently solitary focal individual. This contrasts greatly with RP systems, in which many, perhaps even most, individuals could breed as isolated pairs at a stable equilibrium (dynamic or static), depending upon the distribution of the key resources.

As mentioned above, several previous hypotheses about cooperative breeding and group living have highlighted the importance of variance in patch quality for the occurrence of cooperative breeding and group living (Snapp, 1976; Shields *et al.*, 1988; Stacey and Ligon, 1991; Koenig *et al.*, 1992). However, the effects of such variance have not previously been considered separately for RP versus SB species. Thus, the sociality threshold model yields novel insights about the effects of patch-quality variance on group size distributions. Consider first RP species (Fig. 3a,b). When variance in patch quality is low (Fig. 3a), few patches containing a group of conspecifics would ever exceed the sociality threshold (Δq^*). This is seen in Fig. 3a by noting that any pair of patches whose difference in quality exceeded Δq^* would be extremely rare because one or both of the patches would come from the extreme tails of the patch quality distribution. As a consequence, individuals would be expected to breed solitarily whenever vacant patches were available (i.e. at low population densities). However, if there were extensive variation in patch quality (Fig. 3b), it would be much more likely that a patch containing a group of conspecifics could exceed the sociality threshold relative to vacant patches, and individuals might choose to join groups even if patches of intermediate quality were vacant. In sum, for RP species, increasing variance in patch quality should increase group sizes and the occurrence of groups.

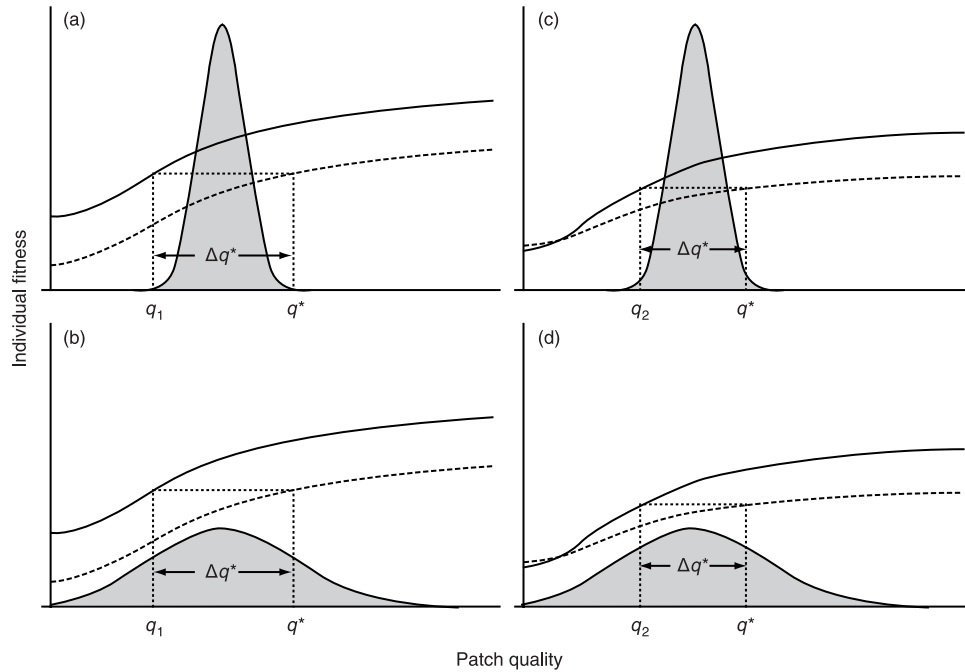


Fig. 3. Effects of patch quality variance in the general sociality threshold model. In all cases, the probability density function for patch quality (shaded region; height scaled for convenient representation) is overlaid on the fitness functions. (a, b) Expected fitness in RP species (lines as in Fig. 2a). (c, d) Expected fitness in SB species (lines as in Fig. 2b). In (a) and (c), there is little variance in habitat quality. Thus, in the RP species (a), few patches with groups of conspecifics would exceed the sociality threshold because the probability that any two patches differ by an amount Δq^* is very small (one or both patches would have to come from the tail extremes of the quality distribution), and thus most individuals would be expected to be solitary unless all patches were occupied. However, in SB species (c), the effect of low variance is the opposite: unoccupied patches rarely exceed the sociality threshold, making colonization and solitary individuals rare. In (b) and (d), there is high variance in habitat quality. This makes it much more likely that individuals in RP species (b) could be favoured to join a group, and individuals in SB species (d) could be favoured to settle solitarily in currently vacant patches.

In SB species, however, the effects of patch quality variance are quite different. In cases when there is little variance (Fig. 3c), a vacant patch will rarely exceed the sociality threshold. Thus, we would expect nearly all new individuals to settle in existing groups, and settlement of new patches should rarely occur. With increasing variance (Fig. 3d), the probability that a vacant patch will exceed the threshold is increased. In SB species, high variance in patch quality should thus increase the likelihood that individuals will breed solitarily in vacant patches. In sum, for SB species, increasing variance in patch quality should decrease group sizes and increase the frequency of solitary breeding, effects that are opposite to those predicted for RP species. Furthermore, if there is a high rate of patch turnover (high temporal patch quality variance), solitary breeding could be frequently observed in spite of the existence of social benefits. By contrast, if there is considerable variance in space but little variance in time, high-quality patches should be quickly

colonized and should build up large groups of individuals, the sizes of which should stabilize over time (due to the feedbacks discussed above). The latter is analogous to hypotheses for the evolution of cooperative breeding and eusociality that suppose that predictable, defensible resources promote stable group living (e.g. Koenig *et al.*, 1992; Jarvis *et al.*, 1994).

Individual group-joining decisions and expected group sizes in any social system thus depend critically on whether groups form due to resource patchiness or social benefits. This may explain why tests of the polygyny threshold and delayed dispersal threshold models have been inconclusive. For example, while the delayed dispersal hypothesis has not been exhaustively tested, tests of the importance of variance in habitat quality have yielded equivocal results (Baglione *et al.*, 2005; Doerr and Doerr, 2006). However, our model may allow the reconciliation of results that heretofore appeared contradictory: in different species the effects of variance in patch quality *should* be different. Species used for any future empirical tests should thus be carefully chosen and classified before making predictions. Furthermore, the more general sociality threshold model provides a single conceptual framework to explain both the occurrence of group breeding in RP species and the unexpected but often documented occurrence of solitary breeding in SB species, which has been even more challenging to understand.

EXAMPLES OF THE INTEGRATED INDIVIDUAL APPROACH

To illustrate the full process-to-pattern approach, we first applied our checklist for designating groups as SB or RP to a variety of taxa and used this classification process to suggest potential cues that individuals in each species might use to make group-joining decisions (Table 1). The three swallow species illustrate that group breeding may be maintained for different reasons in species that are closely related phylogenetically. Table 1 also shows that this classification method can be applied not only to colonial breeders, but also to cooperative and polygamous breeding groups. Once a species has been classified as RP or SB, researchers can test the resulting hypotheses about *which* resource or conspecific cues are used by individuals when making settlement decisions, and thus which benefits could explain the maintenance of group living and patterns of population-level variation. To date, the complete approach, from determining individual decision rules to explaining variation across groups, has been applied to few species (Fig. 4a,b,d). There are additional species for which all elements of the approach are known (Fig. 4c), but researchers worked backwards, describing patterns first, then generating and testing hypotheses about process. The pattern-to-process approach generally spanned multiple studies over at least a decade, while the process-to-pattern approach was accomplished within the context of single 3- to 4-year studies.

Lesser kestrels (Fig. 4a) breed in social groups and as solitary pairs (Serrano *et al.*, 2003), but individuals in large groups have, on average, greater survival probabilities and reproductive success than individuals in smaller groups (Serrano *et al.*, 2004, 2005). Because individuals within large groups enjoy the benefits of predator defence and dilution effects, lesser kestrels are classified as an SB species. As predicted by our RP/SB classification system, individuals use colony size or number of conspecifics as a settlement cue rather than availability of nest sites, and individuals compete to breed in large colonies (Serrano *et al.*, 2004). Young kestrels are usually not successful at settling within larger groups and are forced to settle at nearby smaller-group sites (Serrano *et al.*, 2004; Serrano and Tella, 2007). Thus, individual settlement decisions

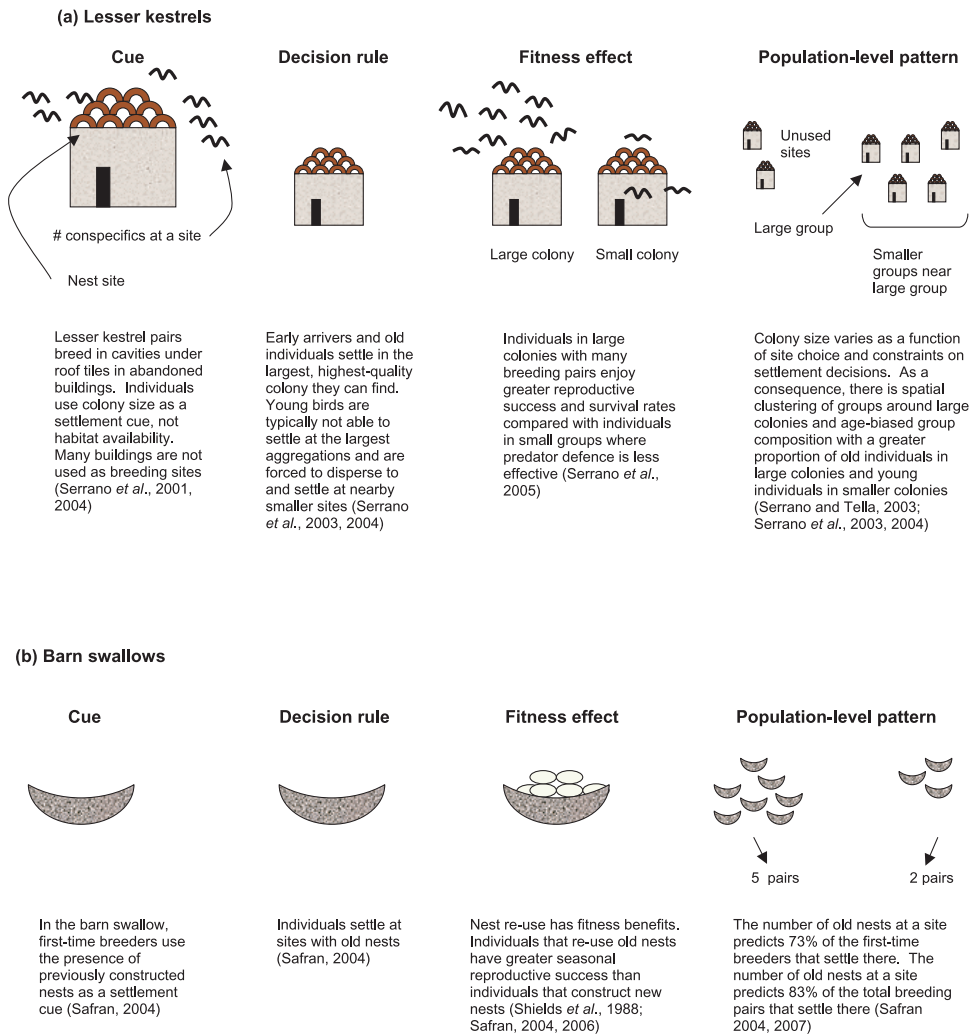
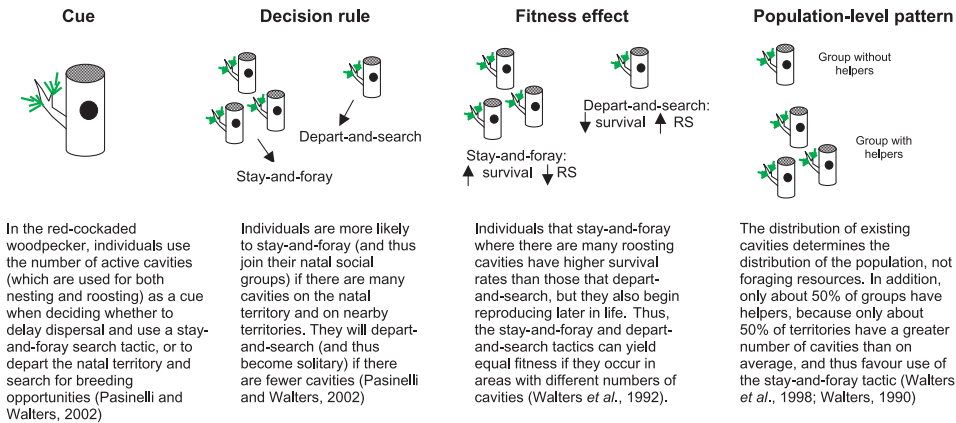


Fig. 4. The integrated individual-based approach: links between the cues and decision rules that individuals use for group formation, the fitness consequences of those decision rules, and larger-scale patterns of group breeding. Examples are provided for: (a) lesser kestrels; (b) barn swallows; (c) red-cockaded woodpeckers, a species in which patterns were studied first and the group formation

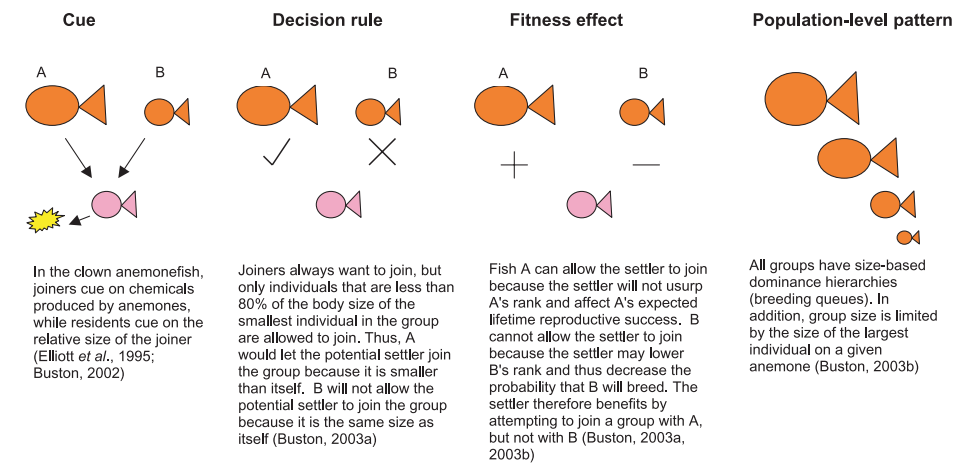
and constraints explain several population-level patterns including the spatial distribution of breeding sites (Serrano and Tella, 2003), variation in colony size, and age distribution across colonies (Serrano *et al.*, 2003, 2004).

A study of barn swallows (*Hirundo rustica*) breeding in colonies provides another example of identifying process first, then predicting pattern (Fig. 4b). The species is classified as RP (Table 1) and, indeed, individuals choose breeding sites based on the presence of old nests. Re-using old nests confers fitness benefits, because individuals that do so start breeding earlier and thus have a higher probability of successfully raising more

(c) Red-cockaded woodpeckers



(d) Clown anemonefish



process has only recently been investigated; and (d) clown anemonefish, a species in which an understanding of the cues and decision rules of multiple types of potential group members was required to predict population-level patterns.

than one brood in a season (Shields *et al.*, 1988; Safran, 2004, 2006). Translating this adaptive individual decision to the population level, the number of old nests at a site explains 83% of the variance in the number of breeding pairs that settle there, and thus explains patterns of variation in colony size (Safran, 2004).

The cooperatively breeding red-cockaded woodpecker (*Picoides borealis*) provides an example in which patterns of group breeding have been known for some time, but the individual-level processes that produce them have only recently been identified (Fig. 4c). In this species, first-year birds search for breeding opportunities using either a stay-and-foray tactic, which involves living on the natal territory and joining the natal social group during

the dispersal period, or a depart-and-search tactic, which does not involve joining a group. Individuals choose their search tactics using the number of active nesting and roosting cavities on the natal and nearby territories as a cue (Pasinelli and Walters, 2002). Birds join the natal social group and stay-and-foray, even though this behaviour increases time to first reproduction when there are a large number of cavities available on the natal territory because cavities confer a survival advantage that balances the immediate reproductive costs (Walters *et al.*, 1992). These adaptive decisions explain both the lack of correlation between the species' distribution and apparently suitable foraging habitat, as well as the unusually low frequency of groups in the population relative to solitary breeding pairs (Walters *et al.*, 1988; Walters, 1990), because groups should only form when the number of suitable cavities is above the average, which should generally occur about 50% of the time. Note that the species can be classified as RP and the classification process suggests that cavities might be used as group-joining cues (Table 1).

Finally, research on the clown anemonefish (*Amphiprion percula*) provides an example of the efficiency of studying process to predict pattern, even in a cooperatively breeding system in which there are social constraints on group choice (Fig. 4d). In this species, the two largest individuals in any group breed, and smaller group members queue in order to eventually become breeders in the group. Potential group joiners initially cue on the presence of an anemone, and existing group members can choose to accept or reject potential joiners (Buston, 2002, 2003a). Thus, the decision rules of both joiners and existing group members must be known to be able to explain population-level patterns. Without social constraints, unattached fish would always benefit from joining groups. However, existing group members will only allow floaters to join if they are less than 80% of the size of existing members and thus do not threaten to usurp their rank in the reproductive queue (Buston, 2003a, 2003b). These decision rules explain the existence of strict size hierarchies within groups as well as patterns of group size, because total group size is limited by the size of the largest individuals in the group (Buston, 2003b).

CONCLUSIONS

Explanations of group breeding must simultaneously predict the decisions individuals make as well as patterns of variability in breeding groups observed at the population level. Empirical research that explicitly links individual-level group-joining processes with population-level patterns is more efficient at elucidating those broader explanations than separate research at each level. We offer three steps for examining the decision rules of individuals and predicting larger-scale patterns.

First, a complete understanding of group formation can only be achieved by understanding settlement decisions and group joining at the individual level. Thus, studies should first identify the settlement cues that individuals use in making these decisions. We suggest that the best way to do this is by distinguishing between resource patchiness and social benefits groups at the outset. Classifying social breeders into SB or RP categories is useful for determining which cues individuals use, which in turn serves as a starting point for understanding patterns of group breeding. This classification encourages field researchers to investigate, early on, whether or not their study animals are benefiting from the presence of conspecifics, and subsequently to design experiments to determine which conspecific benefits explain social breeding (SB groups) or which resources are limiting (RP groups). Second, researchers must verify that settlement decisions based on these cues have

predictable fitness consequences, and are thus subject to natural selection. Finally, once adaptive settlement cues have been identified, researchers should be able to predict population-level patterns in group breeding based on the distributions of settlement cues in the environment. Although we focus on colonial breeding groups, this approach can be applied to other types of vertebrate group-breeding systems including cooperative and polygamous breeding groups.

Examination of links between individual-level decisions and population-level patterns is applicable to a number of behavioural, ecological, and evolutionary issues, including dispersal, life-history evolution, habitat selection, foraging ecology, and sexual selection (Sutherland, 1996; Smith *et al.*, 2000; Cam *et al.*, 2002; Doerr and Doerr, 2004, 2006). Individual behaviour and population patterns are often addressed in isolation from one another, but it is the relationship between these two levels that provides powerful predictive information about the causes and consequences of population dynamics. The approach of determining the relevant cues used in group-formation decisions and how these decisions explain larger-scale patterns of sociality thus provides an exciting research protocol for developing rigorous links between behavioural ecology and population ecology, landscape ecology, and conservation biology.

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