

# Stable group size in cooperative breeders: the role of inheritance and reproductive skew

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Recent studies of reproductive skew have revealed great variation in the distribution of direct fitness among group members, yet there have been surprisingly few attempts to explore the consequences of such variation for stable group size, and none that take into account the future benefits of group membership to nonbreeders. This means that the existing theory is not suited to explain the group size of most cooperatively breeding vertebrates and primitively social insects in which group membership involves substantial future benefits. Here we model the group size of such species as social queues in which nonbreeders can inherit a breeding position if they outlive those ahead of them in the queue. We demonstrate, however, that the results can be generalized to systems in which inheritance occurs via scramble competition, rather than via a strict queue. The model predicts that stable group size will depend on the number of breeding positions in the group and the mortality rates of breeders and nonbreeders, but not on the distribution of reproduction among the pool of breeders. This is because deaths occur at random, so that each individual has the same chance of surviving to reach each breeding position. We tested a specific prediction of the model using data on ovarian development in the paper wasp, *Polistes dominulus*. We found a positive correlation between group size and the proportion of females with fully developed eggs, as predicted. Our results clarify the interaction between the dominance structure and size of animal groups and add to the growing recognition of the potential for inheritance as a major determinant of both individual behavior and group-level characteristics of animal societies. *Key words*: cooperative breeding, dominance, reproductive skew, sociality. [*Behav Ecol* 17:560–568 (2006)]

Considerable debate in recent years has surrounded attempts to understand the causes of variation in the distribution of reproduction, or degree of reproductive skew, among members of cooperative animal societies (Keller and Vargo 1993; Johnstone 2000; Reeve and Keller 2001). After a flurry of theoretical work, the topic has become saturated with competing models that differ in their assumptions about the mechanisms by which one animal might control the reproduction of another and about the options that individuals may have outside the group (reviewed by Johnstone 2000; Magrath et al. 2004; Cant 2006). This preoccupation with the evolutionary causes of variation in skew has diverted attention from the consequences of such variation for the major characteristics of social groups. In particular, a theoretical lacuna has arisen between skew theory, focusing on variation in fitness among group members, and group size theory, which typically assumes that such variation is absent, measuring instead the benefits of group membership on a per-capita basis (Pulliam and Caraco 1984; Giraldeau 1988). The question of how variation in the number of breeders per group and the distribution of reproduction among them should affect stable group size remains largely unexplored.

To date the only models to explore the link between skew and stable group size assume that animals join groups on the basis of the current costs and benefits of group membership (Giraldeau 1988; Hamilton 2000; Reeve and Emlen 2000). For example, Reeve and Emlen (2000) solve for stable group size from the perspective of a single dominant who can offer shares of reproduction as recruitment incentives to potential joiners. Because only current benefits are considered, a dominant who has full reproductive control can deter unwanted joiners simply by withholding reproductive shares, and thus in

this model groups never grow larger than that which is optimum for the dominant (the “saturated” group size). In most cooperative vertebrates and many primitively social insects, however, subordinates apparently remain in or join groups as nonbreeders in expectation of inheriting a breeding position in the future (e.g., Strassmann and Meyer 1983; Samuel 1987; Hughes and Strassmann 1988; Field et al. 1999; Monnin and Ratnieks 1999; Cant and Field 2001 in Hymenoptera; and Wiley and Rabenold 1984; Stacey and Koenig 1990; Emlen 1991; Creel and Waser 1994; Poston 1997; East and Hofer 2001; Buston 2003, 2004 in vertebrates). Where subordinates join for future benefits, manipulation of the current distribution of reproduction cannot be used as a means to control group size. This is because subordinates will favor group membership even if they obtain no current direct or indirect fitness (Kokko and Johnstone 1999; Ragsdale 1999). Groups will thus grow larger than the size that is optimal for the dominant, or for that matter, any of the other subordinates. The question is, at what size will these groups stabilize?

In this paper we explore the question of stable group size when subordinates join for future fitness benefits. We model cooperatively breeding groups as queues in which new individuals join the bottom of the queue as nonbreeders but can inherit breeding status if they outlive those ahead of them in the queue (Cant and Field 2001, 2005; Shreeves and Field 2002; Cant, Llop, and Field forthcoming). As attested by the variety of skew models on offer, there are many potential causes of variation in the distribution of reproduction, but here we focus exclusively on the consequences of such variation for the economics of joining decisions. We assume that conflict over the number of breeding positions and the distribution of reproduction among them is resolved in some unspecified way first, and then subordinates use information about the reproductive structure of the group to decide whether or not to join. This approach, in which the joining decision of a nonbreeder depends on the distribution of reproduction in the group, but not vice versa, makes biological sense where subordinates join as nonbreeders in expectation of future fitness because

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dominants cannot deter joiners by denying them a share of current reproduction, nor can they make credible “promises” of reproduction in the future. Such promises of reproduction would require a form of binding or self-enforcing commitment (Nesse 2001; McNamara and Houston 2002), for which it is difficult to hypothesize a plausible mechanism.

The aim of constructing the model was to generate simple, testable predictions about the relationship between stable group size, the proportion of breeders in the group, and the way in which reproduction is shared among them. After we had derived these predictions, we set out to test them by examining the relationship between the proportion of breeders and group size in a model social system, the paper wasp, *Polistes dominulus*.

**THE MODEL**

We consider a group of size  $n$  in which  $b$  are breeders and the remaining  $s$  are nonbreeders. The proportion of breeders in the group will be denoted  $q$  ( $=b/n$ ).

All group members form a strict queue or hierarchy in which an individual moves up one rank if any individual ahead of it in the queue dies. Thus, an individual can move from rank  $i$  to  $i - 1$  on the death of any of the  $i - 1$  individuals ahead of it in the queue. It will be shown, however, that our results can be generalized to other systems of inheritance, such as scramble competition (Appendix A).

Our analysis proceeds in 2 steps. First we derive an expression for the lifetime fitness that an individual can expect on becoming a breeder and then go on to consider the profitability of joining groups of different sizes and hence stable group size.

**Expected breeder fitness and reproductive skew**

Let the total reproductive output of the group  $G(b, n)$  (abbreviated to  $G$ ) be a function of both total group size  $n$  and the number of breeders in the group  $b$ . This productivity function may arise as a result of active helping behavior or simply through passive grouping effects. We make no assumption about whether total productivity increases or decreases with the number or proportion of breeders in the group. Within the pool of  $b$  breeders, the breeder at rank  $i$  suffers an instantaneous mortality rate  $m_i$  and contributes a fraction  $f_i$  toward the total group output ( $\sum_1^b f_i = 1$ ).

Let  $w_i$  denote the expected direct fitness of a breeder at rank  $i$  ( $\leq b$ ) in a group of total size  $n$ , which is equal to its current reproductive output at rank  $i$  plus its expected reproductive output in the future if it survives to move up in rank. This expected fitness can be written as the recursion relation

$$w_i = f_i t_i G + p_{i \rightarrow i-1} w_{i-1}. \tag{1}$$

Here,  $t_i$  is the period that a breeder can expect to stay at rank  $i$  and  $p_{i \rightarrow i-1}$  is the probability that the individual at rank  $i$  survives to ascend to rank  $i - 1$ . The period  $t_i$  is equal to the time until the first death in the subqueue of individuals from rank  $i$  upward. This is given by the inverse of the sum of death rates of the individuals in the subqueue, that is,

$$t_i = \frac{1}{\sum_1^i m_j}, \tag{2}$$

where  $m_j$  is the instantaneous mortality rate associated with rank  $j$ .

We assume that mortality depends on rank only. In this case the probability that an individual is the first to die in the

subqueue of individuals of ranks  $i$  to 1 is  $m_i / \sum_1^i m_j$ . Thus, the probability that the individual at rank  $i$  survives to move up one place is equal to  $1 - (m_i / \sum_1^i m_j)$  or

$$p_{i \rightarrow i-1} = \frac{\sum_1^{i-1} m_j}{\sum_1^i m_j}. \tag{3}$$

Substituting Expressions 2 and 3 into Equation 1, the expected fitness on reaching the top breeding rank is

$$w_1 = \frac{f_1 G}{m_1}, \tag{4a}$$

from which we can write the expected fitness on reaching breeding rank 2 as the recursion relation

$$w_2 = \frac{f_2 G}{m_1 + m_2} + \left[ \frac{m_1}{m_1 + m_2} w_1 \right], \tag{4b}$$

the expected fitness on reaching rank 3 as

$$w_3 = \frac{f_3 G}{m_1 + m_2 + m_3} + \left[ \frac{m_1 + m_2}{m_1 + m_2 + m_3} w_2 \right], \tag{4c}$$

and so on up to the last breeder rank

$$w_b = \frac{f_b G}{\sum_1^b m_j} + \left[ \frac{\sum_1^{b-1} m_j}{\sum_1^b m_j} w_{b-1} \right].$$

This is the fitness payoff associated with inheriting the lowest ranked breeding position in the group or, in other words, the payoff of becoming a breeder. By substituting Equation 4a into 4b, and then Equation 4b into 4c, and so on this last expression simplifies to

$$w_b = \frac{\sum_1^b f_j G}{\sum_1^b m_j} = \frac{G}{\sum_1^b m_j}. \tag{5}$$

Notice that each  $f_i$  cancels out of this expression. Thus, the lifetime fitness payoff associated with becoming a breeder is independent of the reproductive skew among breeders. This makes intuitive sense: reproduction may be skewed toward particular breeding ranks, but because each new breeder shares an equal chance of attaining those ranks, the lifetime payoff of becoming a breeder is independent of the skew among breeders. This argument also holds if breeders compete at random for each breeding vacancy that arises (Appendix A). This means that the degree of skew among breeders can have no impact on whether a potential recruit joins or not. Rather, the payoff associated with becoming a breeder depends only on the number of breeders and the mortality rates associated with each breeding rank, as evident from Expression 5.

It should be pointed out that the above argument assumes that mortality rate depends on rank only and is independent of, or linearly related to, reproductive share. It may be, however, that energy invested in reproduction decreases survivorship, such that mortality rate is a nonlinear increasing function of reproductive share. If mortality is an increasing accelerating function of reproductive share (i.e.,  $\partial^2 m / \partial f^2 > 0$ ), any skew in reproduction toward the top ranks increases the relative value of the lower breeding ranks, which in a strict queue, are precisely those ranks to which a new joiner is most likely to accede. Thus, the payoff of becoming a breeder (and thus, by the reasoning developed below, stable group size) will not be independent of skew in these circumstances but will increase as the distribution of reproduction becomes skewed

toward the top breeding ranks. The opposite pattern will hold where mortality is an increasing, decelerating function of reproductive share ( $\partial^2 m / \partial f^2 < 0$ ). We do not explore this effect further here.

### Stable group size

Now consider the decision of a potential recruit of whether to join the group at rank  $n$  or disperse to breed independently elsewhere. These potential recruits can be thought of as newly matured offspring faced with the decision of whether to remain in their natal group or as adult “floaters” trying to gain access to a breeding territory. For simplicity, we assume initially that group members are unrelated, but in a later section we show that incorporating relatedness does not affect our main results.

Individuals are assumed to join groups whenever it is profitable for them to do so, that is, groups form by free entry of individuals from outside (Sibly 1983; Pulliam and Caraco 1984; Giraldeau 1988; but see Higashi and Yamamura 1993 for an alternative approach). This approach allows us to solve for the stable group size from the perspective of a joiner, that is, the maximum-sized group that a subordinate will be selected to join. Under rules of free entry, groups are expected to grow in size until the payoff to the joiner of joining just equals that it would get from dispersing.

Let the expected fitness of the dispersal option be denoted  $x$ . Then the fitness payoff of joining the group at rank  $n$  is

$$W_n = p_{n \rightarrow b} w_b, \quad (6)$$

where  $p_{n \rightarrow b}$  is the probability that the joiner at rank  $n$  survives to enter the breeder pool at rank  $b$ . We will hereafter refer to  $W_n$  as the “joiner’s payoff.” We can now define the stable group size,  $n^*$ , as that for which

$$W_n - x = 0.$$

Note that Expression 6 implies that the joiner expects to inherit a group of the same size that it joins (because  $w_b$  is calculated on the basis of  $n$ ). It may be, however, that individuals join groups in the expectation that conditions will improve or deteriorate, in which case we would expect stable group size to be somewhat larger than  $n^*$  in the former case and smaller than  $n^*$  in the latter (see also Shreeves and Field 2002).

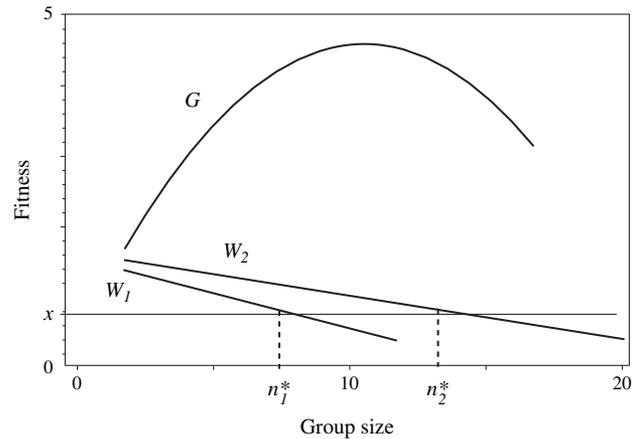
We know from the first section that the number of breeders in a group of given size, rather than the degree of reproductive skew among them, determines the payoff of becoming a breeder and thus the payoff of joining a queue to inherit breeding status. The question of interest, therefore, is how stable group size should vary with the number or, equivalently, the fraction of breeders in the group. We present our results in terms of the fraction of breeders  $q$  rather than the number as this is a more useful focal parameter for comparison across group sizes: total group size will necessarily increase with breeder number even if the number of nonbreeders in the queue remains constant.

Our model is simplified by assuming that breeders suffer equal mortality rates  $m_B$  and nonbreeders suffer equal mortality rates  $m_S$ . Expression 5 for the expected payoff of becoming a breeder becomes

$$w_b = \frac{G}{qn m_B} \quad (7)$$

and the probability of inheritance  $p_{n \rightarrow b}$  is given by

$$p_{n \rightarrow b} = \frac{q m_B}{q(m_B - m_S) + m_S}. \quad (8)$$



**Figure 1**

Stable group size when individuals queue as nonbreeders. Total productivity  $G$  and the expected payoff to an individual joining the bottom of the queue  $W$  are shown as a function of group size for 2 values of the nonbreeder mortality rate  $m_S$  ( $m_1 = 0.9$ ,  $m_2 = 0.5$ ). The stable group size is that at which the joiner’s payoff equals the payoff it could expect from dispersal ( $x$ ). Note that in some cases, for example, high probability of dispersal or high mortality inside the group relative to that outside, groups can stabilize at a size less than that which is most productive. (Other parameter values used to draw the figure:  $m_B = 0.5$ ,  $j = -0.1$ ,  $k = -0.05$ ,  $q = 0.3$ ).

Note that this expression is independent of  $n$ . In Appendix A we show that the same expression for the probability of inheritance holds for a scramble system in which each nonbreeder competes on equal terms with all the others for each breeding vacancy that arises. Thus, our results concerning stable group size will hold whether group members form a strict queue or compete at random for breeding positions.

Substituting Equations 7 and 8 into Equation 6 we have

$$W_n = \frac{G}{n(q(m_B - m_S) + m_S)}. \quad (9)$$

This joiner’s payoff is plotted in Figure 1 for a particular quadratic function  $G$ :

$$G(q, n) = n(1 + jq + kn). \quad (10)$$

In this function  $j$  measures the effect cobreeders have on each other’s reproductive success. Where  $j$  is positive, each breeder benefits synergistically as the fraction of breeders increases; where  $j$  is negative, each breeder does worse as the fraction of breeders increases. The parameter  $k$  is a measure of the costs of crowding due to increases in group size per se: this parameter is assumed negative so that group productivity must at some point start to decline with increasing group size. In the example shown we have assumed that the proportion of breeders  $q$  remains constant as the group grows, but similar plots are obtained if we assume that  $q$  changes as  $n$  changes (as would be the case, e.g., if the number of breeders was fixed).

### Solving the model

Subtracting  $x$  from the right-hand side of Equation 9, setting equal to zero, and solving for  $n$  yields the following expression for stable group size:

$$n^* = \frac{G}{x(q(m_B - m_S) + m_S)}. \quad (11)$$

The stable group size must satisfy the above relation, but the solution is implicit because productivity  $G$  is a function of group size. Moreover, the value of  $n$  for which Relation 11 is satisfied is itself a function of the fraction of breeders  $q$ . Before focusing on the relationship between  $n^*$  and  $q$ , therefore, it helps to write the functions in Equation 11 in full as

$$n^*(q) = \frac{G(q, n^*(q))}{x(m_S + q(m_B - m_S))} \quad (12)$$

Treating group size as a continuous variable, we can differentiate with respect to  $q$  and rearrange in terms of  $\partial n^*(q)/\partial q$  to obtain the desired relationship between  $n^*$  and  $q$ :

$$\frac{\partial n^*(q)}{\partial q} = \frac{G(q, n^*(q))(m_S - m_B) + \frac{\partial G(q, n^*(q))}{\partial q} A}{A \left( Ax - \frac{\partial G(q, n^*(q))}{\partial n^*} \right)}, \quad (13)$$

where  $A = q(m_B - m_S) + m_S$ , which is always positive given  $0 < q < 1$ .

At the stable group size, the denominator of Equation 13 is positive (see Appendix B). Thus, the sign of  $\partial n^*/\partial q$  will be the same as that of the numerator of Equation 13. This also means that neither dispersal fitness  $x$  nor the magnitude of the slope  $\partial G/\partial n^*$  have any influence in determining the sign of the slope  $\partial n^*/\partial q$ .

Before plotting the sign of Equation 13 we first define a new variable, relative mortality ( $\theta$ ) as

$$\theta = \log_e(m_S/m_B).$$

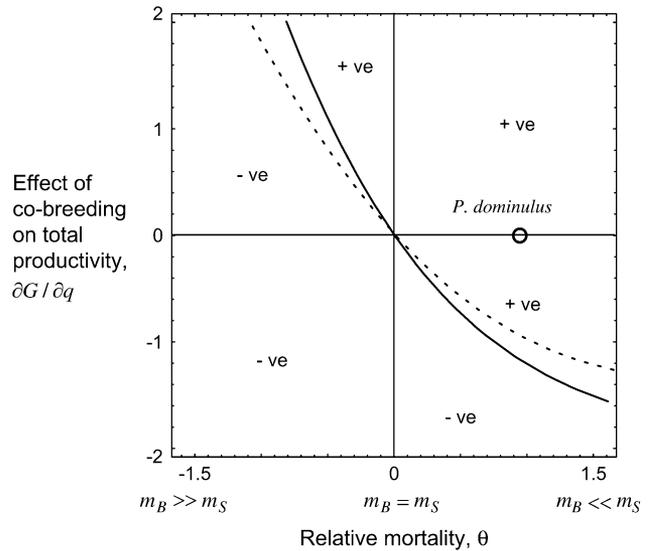
Positive values of  $\theta$  imply that the mortality rate of breeders is lower than that of nonbreeders; negative values imply the opposite, and  $\theta = 0$  where mortality rates are equal.

Figure 2 shows a contour plot of the sign of  $\partial n^*/\partial q$  as a function of  $\partial G/\partial q$  and relative mortality  $\theta$ . The solid line defines the threshold at which  $\partial n^*/\partial q$  is equal to zero. We can summarize the results shown in Figure 2 by noting that 1) stable group size increases with the fraction of breeders where  $m_B < m_S$  and decreases with the fraction of breeders where  $m_B > m_S$ , in cases where the slope of total productivity versus the fraction of breeders is close to zero, and 2) stable group size increases with the fraction of breeders where the sign of  $\partial G/\partial q$  is positive, and decreases with the fraction of breeders where the sign of  $\partial G/\partial q$  is negative, in cases that the mortality rates of breeders are similar.

This pattern is illustrated further in Figure 3, where we plot stable group size as a function of the fraction of breeders for our quadratic productivity function 10. In this function the parameter  $j$  gives the slope  $\partial G/\partial q$ . In line with the predictions of Figure 2, the slope of the relationship between stable group size and the proportion of breeders flips around, depending on whether  $\theta$  (Figure 3a) and  $\partial G/\partial q$  (Figure 3b) are positive or negative.

**Relatedness**

Most cooperatively breeding groups to which this model applies are not composed of unrelated individuals, so it is natural to consider indirect fitness influences on the costs or benefits of joining a group of relatives. In this section, therefore, we briefly explore the effects of relatedness in the model. Let all group members be symmetrically related by coefficient  $r$ . We assume that where a focal individual chooses to disperse groups are temporarily reduced by one member, and there is a corresponding change in the total group productivity of current breeders from  $G(q, n)$  to  $G(q, n - 1)$  until the group recovers from the loss of the disperser (these productivities

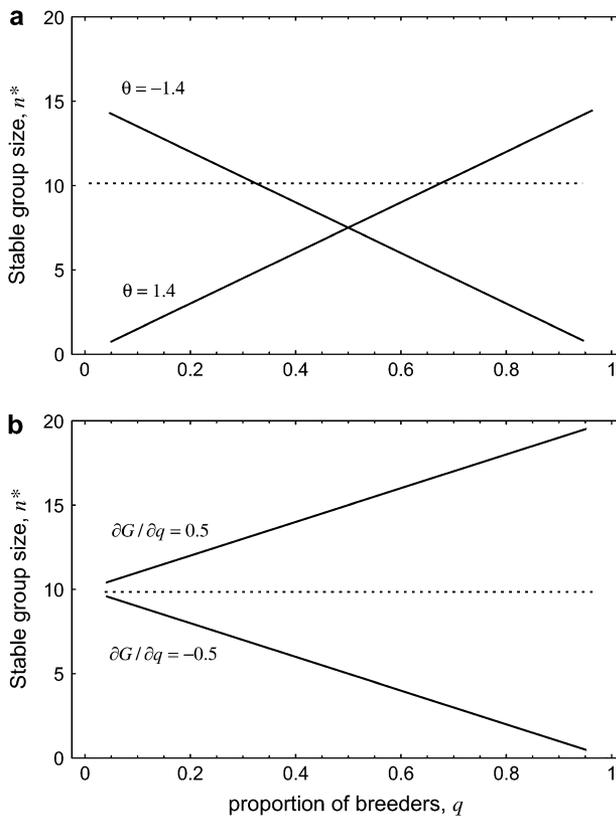


**Figure 2** Contour plot showing the sign of the predicted relationship between stable group size and the proportion of breeders when group members are unrelated to each other (solid line) and when they are related by  $r = 0.5$  (dotted line). The y axis measures the slope of the relationship between total productivity ( $G$ ) and the fraction of breeders ( $q$ ): positive values indicate that total productivity increases with  $q$ , negative values imply that total productivity decreases with  $q$ . The x axis measures the log of the relative mortality rates of breeders ( $m_B$ ) and nonbreeders ( $m_S$ ). Negative values of  $\theta$  imply that the mortality rate of breeders is greater than that of nonbreeders; positive values imply the opposite. Regions where stable group size is predicted to increase with the proportion of breeders in the group are marked with a positive (+ve) symbol; in this region low-skew groups are predicted to be larger than high-skew groups. Regions where stable group size decreases with the proportion of breeders in the group are marked with a negative (-ve) symbol; in this region low-skew groups are predicted to be smaller than high-skew groups. Contours are drawn along the line where the slope of this relationship is zero. Also marked as a small circle is the region of parameter space that applies to *Polistes dominulus* based on field data of mortality rates of highest and lowest ranking individuals in cofoundress associations. The contour for  $r = 0.5$  is drawn assuming  $\partial G_{n-1}/\partial q = 0.8\partial G_n/\partial q$ , that is, that adding one group member results in a 25% increase in the sensitivity of total productivity to changes in the fraction of breeders. Other values used to draw the figure:  $q = 0.1$ ,  $G_n = 1.8$ ,  $G_{n-1} = 2$ ,  $\alpha = 1.5$ .

will be abbreviated to  $G_n$  and  $G_{n-1}$ , respectively). The indirect fitness impact of the decision to stay in the group at rank  $n$  rather than disperse is therefore equal to

$$r\alpha(G_n - G_{n-1}),$$

where  $\alpha$  is a control parameter that measures the duration for which the dispersing individual's loss affects group productivity. Values of  $\alpha < 1$  imply that the group recovers from the loss of the dispersing individual before the next death in the group of  $n - 1$ , so that only current breeders experience a change in productivity as a result of the decision to disperse. Values of  $\alpha > 1$  imply that the disperser is not replaced until after the first death in the group  $n - 1$ , so that both current and future breeders are impacted by the change in productivity. This approach, although simplistic, is sufficient to yield insight into the directional effects of relatedness on the relationship between group size and the fraction of breeders when joining decisions have indirect fitness consequences. Moreover, as we shall see, incorporating relatedness in this way has negligible effects on our main results, suggesting that



**Figure 3**

Stable group size as a function of the proportion of breeders in the group (a) for 2 values of relative mortality,  $\theta$ , and (b) for 2 values of the slope of total productivity against the proportion of breeders in the group. The most productive group size is marked as a dotted line. As indicated in Figure 2, the direction of the relationship between  $n^*$  and  $q$  flips around depending on the sign of  $\theta$  and  $\partial G/\partial q$ . The function  $G$  in this example is  $G = n(1 + jq - kn)$ . The parameter  $j$  gives the slope  $\partial G/\partial q$ . Other values: (a)  $x = 0.5$ ,  $k = 0.05$ ,  $\partial G/\partial q = 0$ ; (b)  $x = 0.5$ ,  $k = 0.05$ ,  $\theta = 0$ .

our analysis above based on nonrelatives captures the main influences on the relationship between stable group size and the proportion of breeders in the group.

Given these assumptions, we can write the inclusive fitness payoff to a focal individual of joining versus dispersing as

$$I_n = p_{n \rightarrow b} w_b - x + r\alpha(G_n - G_{n-1}). \quad (14)$$

The stable group size in this case is that for which  $I_n = 0$ . Note that in our model ( $G_n - G_{n-1}$ ) can be positive or negative at the stable group size, so the relationship between  $r$  and the stable group size may also be positive or negative depending on the value of the other parameters. This contrasts with other “free-entry” models of stable group size based on current costs and benefits that would predict a negative relationship between  $r$  and  $n^*$  because in these models ( $G_n - G_{n-1}$ ) is always negative at the stable group size (Sibly 1983; Pulliam and Caraco 1984; Giraldeau 1988).

We proceed as before by substituting Equations 7 and 8 into Equation 14, setting equal to zero, and solving for  $n$  to give an implicit expression for  $n^*$ . We can then differentiate this expression with respect to  $q$  rearrange to yield an expression  $\partial n^*/\partial q$  and plot the zero contour of  $\partial n^*/\partial q$  as in Figure 2. It turns out that where  $\partial G_n/\partial q$  and  $\partial G_{n-1}/\partial q$  are equal, that is, a change in the proportion of breeders has the same proportional impact on productivity in a group of size  $n$  as in a group of size  $n - 1$ , the contour of the relatedness model coincides

exactly with that of the model based on nonrelatives, regardless of the value of the control parameter  $\alpha$ . Where the productivity impact of a change in the fraction of breeders is different at different group sizes (i.e.,  $\partial G_n/\partial q \neq \partial G_{n-1}/\partial q$ ), the contours of the 2 models diverge slightly, with the degree of divergence increasing with the control parameter  $\alpha$ . An example is shown in Figure 2. We can conclude that incorporating relatedness slightly alters the location of the threshold values of  $\partial G_n/\partial q$  and  $\log_e(m_s/m_B)$  for which  $\partial n^*/\partial q$  is positive or negative, but the main predictions of the model are unchanged.

The general pattern of a diagonal contour passing through the origin held across all values of  $r$  that we tested.

### GROUP SIZE AND OVARIAN DEVELOPMENT IN *POLISTES DOMINULUS*

We tested a specific prediction of the model using the paper wasp, *P. dominulus*, by examining the correlation between the proportion of females in each group with developed ovaries and group size. This species fits the assumptions of the model reasonably well. Nests are founded each spring at our study site in southern Spain by overwintered foundresses, usually full sisters (Cant and Field 2001; Shreeves et al. 2003). Foundresses form a linear dominance hierarchy in which only high-ranking females reproduce, but low-ranked individuals can inherit the position of breeder if they outlive those above them in the queue (Queller et al. 2000; Cant and Field 2001). Cofoundress associations at the site exhibit a wide range of group sizes: 18 cofoundress nests collected prior to worker emergence ranged in size from 2 to 13 females (mean 4.8). At this time group membership is stable except for deaths due to predation while foraging (Cant and Field 2001). Data on both helping effort and aggression suggest that individuals possess information on their own relative ranking in the inheritance hierarchy and adjust their behavior accordingly (Cant and Field 2001, 2005; Cant, Llop, and Field forthcoming).

It should be noted that information on the correlation between the proportion of reproductive females per group and stable group size can at best offer only limited support for the model because we are unable to determine the direction of causality in the relationship. Nevertheless, 2 features of this system allow us to make a strong prediction about the sign of this correlation; hence, there exists the opportunity to falsify a key prediction of the model. First, productivity in *Polistes* is likely determined by the number of cells in the nest, rather than by the number of females that breed (Reeve 1991; Field et al. 1998). Thus, it is probably safe to assume that the value of  $\partial G/\partial q$  is not far from zero. Second, high-ranking females spend less time off the nest foraging and experience lower mortality than low-ranking females (Cant and Field 2001). Indeed, the mortality rate of the lowest ranked females in a group is more than twice that of the highest ranked individual in the same group (2.8;  $N = 10$  nests; M Cant and J Field, unpublished data). This gives us an approximate value of  $\log_e(m_s/m_B)$ , and so we can locate the parameter space of the model that applies to this species. This area is marked on Figure 2. We can therefore make the strong prediction from our model that there should be a positive relationship between the fraction of females that breed in each group and stable group size in this species.

### Methods

To test this prediction we examined ovarian development in all 101 foundresses from 18 nests collected just prior to the emergence of workers. Wasps and nests were collected from

our field site near Conil de la Frontera, Cadiz, Spain, in spring 2000 and 2003. We captured all the foundresses on each nest before dawn when it was too cold for the animals to fly away. Group size was taken as the number of individuals present when the nest was collected, just prior to worker emergence. All nests contained pupae at the time of collection and so were at the same developmental stage. Nests on which workers were already present were excluded from the analysis because worker emergence typically coincides with the disappearance of many of the original foundresses (Reeve 1991; Gamboa et al. 1999; M Cant and J Field, personal observations). After collection, wasps and nests were immediately frozen for later dissection and DNA analysis.

We measured ovarian development in July and August 2004. Abdomens were dissected in 1% saline solution and measurements taken through a dissecting microscope at either  $\times 25$  or  $\times 50$ . We scored ovarian development on a scale of 0–3 and measured the length of the largest egg, if any measurable eggs were present. We classed foundresses as potential breeders if one or more ovarioles contained eggs of a “layable” size. This layable size was taken as the minimum size of 20 laid eggs extracted from nests of the same population.

To test the sign of the relationship between group size and the proportion of breeders in the group, we used both simple linear regression on arcsine-transformed proportion data with group size as the response variate and generalized linear model with binomial errors and number of breeders/group size as the response variate (Genstat 6.0). In this model, group size and date of collection were fitted as independent continuous variables and year (2000 or 2003) as a factor. Terms were dropped from the model until further removals led to significant ( $P < 0.05$ ) increases in deviance, as assessed against tabulated values of  $\chi^2$ .

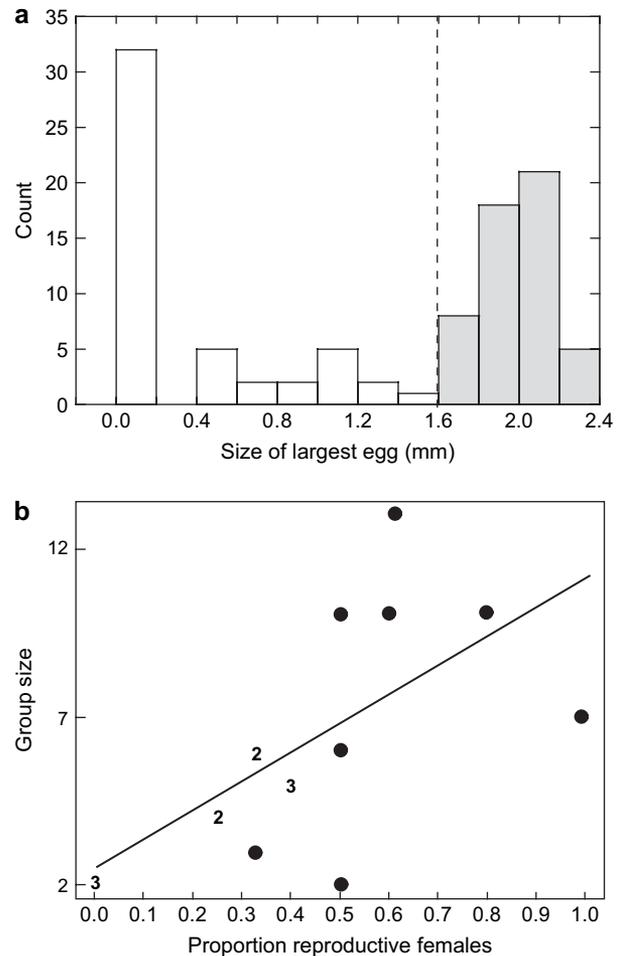
## Results

Cofoundresses exhibited wide variation in the degree of ovarian development and egg production. Among the sample of 101 foundresses dissected, 69 (68%) carried recognizable and measurable eggs in one or more ovarioles. Of these 69 females, 52 (75%) possessed eggs of layable size (i.e.,  $\geq 1.6$  mm). Thus, 52/101 (51%) of females were classed as potential breeders. The distribution of largest egg sizes was bimodal, with an identifiable threshold dividing these females with fully developed eggs from those with little or no egg development (Figure 4a).

Group size increased with the proportion of females classed as potential breeders on the basis of largest egg size (linear regression:  $F_{1,17} = 16.36$ ,  $P = 0.001$ ; Figure 4b). The relationship remained significant after we excluded 3 nests (each of 2 foundresses) that had no identifiable egg layer on the basis of largest egg size ( $F_{1,14} = 5.37$ ,  $P = 0.03$ ). In the generalized linear model, only group size caused a significant increase in deviance when dropped from the model for all 18 nests ( $\chi^2_1 = 9.69$ ,  $P = 0.002$ ) and for the 15 nests with at least one potential breeder ( $\chi^2_1 = 5.31$ ,  $P = 0.02$ ). We conclude that data on ovarian development in this species are consistent with our prediction of a positive relationship between stable group size and the proportion of breeding females in the group.

## DISCUSSION

We have shown that, in a strict linear hierarchy, the distribution of reproduction among breeders has no impact on the decision of a nonbreeder to whether to join a queue to inherit a breeding position rather than disperse to breed elsewhere. The degree of skew among “breeders,” therefore, has no impact on stable group size in such cases. This is because each



**Figure 4**

(a) Size distribution of the largest eggs present in ovarioles of 101 dissected foundresses from 18 groups. Shaded bars are those females classed as breeders on the basis of largest egg size. (b) Observed group sizes in 18 foundress associations of *Polistes dominulus* versus the proportion of females in the group with fully developed eggs. Each point represents a nest. Numbers indicate multiple nests at the same point. The sign of the least squares regression matches the prediction of Figure 2 ( $y = 2.18 + 865x$ ,  $r^2 = 0.46$ ,  $P = 0.001$ ).

new joiner has the same chance of surviving to reach each breeding position, so biases between ranks in reproductive shares do not affect the expected lifetime fitness of a new recruit. Rather, the factors influencing the expected fitness of a joiner to a group of a given size are the relative number of breeders compared with nonbreeders and the mortality rates of different ranks in the group.

Because joining decisions depend primarily on the relative number of breeders, we have focused on elucidating the relationship between the fraction of breeders in the group and stable group size. The model predicts a positive relationship between stable group size and the fraction of breeders where (1) breeders have a synergistic effect on each other's reproduction and/or (2) the mortality rate of breeders is less than that of nonbreeders. (Conversely, a negative relationship between group size and the fraction of breeders is expected where cobreeding is costly and breeders suffer elevated mortality.) Result (1) is intuitive because, where total productivity increases with the proportion of breeders, the payoff to a potential joiner is also an increasing function of the fraction of breeders, so groups are expected to stabilize at a larger size. Result (2) holds because reduced breeder mortality increases

the value of each breeding position relative to each nonbreeding position, so again groups with a larger proportion of breeders become more profitable to join overall, leading to an increase in stable group size.

The model extends and clarifies previous arguments about the relationship between the power structure of groups and the stable group size. For example, Giraldeau (1988) uses a graphical model to argue that despotic groups, in which resources are monopolized by one or a few individuals, will be smaller than egalitarian groups because joiners to the latter group will receive a greater payoff. This is true if joining decisions are based on current fitness only and there is no possibility of inheritance, as in the foraging situations addressed by Giraldeau (1988). In queuing systems, however, where joining decisions are based on inheritance prospects, egalitarian groups may be less attractive to a potential joiner than despotic groups. This is because the huge payoff of becoming the sole breeder in a despotic group may more than make up for the relatively low probability of reaching that position. By contrast, a subordinate joining an egalitarian group has a relatively high chance of inheriting one of the many breeding positions, but on doing so its offspring will face competition from those of other breeders for access to group resources. As we have demonstrated, the relative profitability of the 2 groups depends on the level of competition between co-breeders and the mortality rates of breeders and nonbreeders.

In the context of reproductive skew, concession models assume that a dominant can use its control over reproductive shares to optimize group size (Reeve and Emlen 2000). In our framework, by contrast, only current breeders compete for reproductive shares (by whatever means), whereas nonbreeders join groups in expectation of competing for reproduction in future, pushing group size above that which is optimum for breeders. Data from cooperatively breeding vertebrates suggest that groups do indeed grow to a size at which the survivorship of offspring starts to decline (e.g., Seychelles warbler, Komdeur 1994; banded mongooses, Gilchrist 2001; suricates, Russell et al. 2002). Moreover, widespread accounts of forcible eviction in cooperatively breeding vertebrates and insects indicate that groups in nature often exceed the most profitable size, at least from the perspective of the evictors (see Johnstone and Cant 1999 and references therein). These incidences of eviction are not easily accommodated by concession models of skew because a dominant in these models can deter a subordinate from joining simply by withholding a share of reproduction. At the same time, however, such observations of eviction challenge our assumption that groups form by free entry. Where current breeders can evict or defend the group against potential joiners, stable group size will reflect a compromise between the interests of “insiders” and “outsiders” (Higashi and Yamamura 1993). We can expect such group defense by breeders to reduce the area of parameter space for which group size increases with the proportion of breeders because groups with many breeders, while being more attractive to joiners, will also be better able to defend against them.

The model is primarily designed with single-sex aggregations in mind, but it is interesting to consider mixed-sex societies in which males and females may have separate queues. In this case we need to solve for the stable number of males and the stable number of females simultaneously. For the female queue, a change in the fraction of breeders  $q_f$  will lead to a change in stable number of females in the manner shown in Figure 2. This will cause both a change in total group size  $N$  and a potential change in the fraction of male breeders because  $q_f$  and  $q_m$  will often be positively correlated (unless there is full control of females by dominant males). The fraction of male breeders per se, however, is unlikely to affect total productivity because male breeders simply compete for a share of

paternity but their number does not change the number of young produced. For this reason, it turns out that for a quadratic productivity function the sign of the relationship between total stable group size (i.e., stable number of males + stable number of females) is independent of the fraction of male breeders  $q_m$ . Rather, total stable group size, stable number of males, and stable number of females all vary with the fraction of female breeders in the manner shown in Figure 2 (unpublished simulations). The predictions of the single-sex model may therefore apply well to mixed-sex groups.

Data on ovarian development in *P. dominulus* support the prediction of our model regarding the relationship between group size and reproductive structure in this species. Care must be taken when interpreting this result, however, because we are unable to test for the direction of causality in the relationship. In particular, it is possible that large group size caused an increase in the proportion of individuals that reproduced, and not vice versa. For example, dominant females may be less able to suppress reproduction of subordinates in large groups, generating a positive correlation between group size and the fraction of females that breed. This possibility does not enter into our model because we explicitly assume that stable group size depends on the number of breeding positions, but not vice versa. In *Polistes* it seems unlikely that increases in group size per se should lead to a break down in dominant control, unless larger groups possess stronger subordinates. This is because breeding opportunities are probably set primarily by the number of cells and dominants patrol the nest continuously (Reeve 1991; Reeve and Ratnieks 1993). Indeed, in *Polistes bellicosus*, Field et al. (1998) found that the proportion of reproduction obtained by the dominant individual increased rather than decreased with group size. In other cooperatively breeding species, however, and vertebrates in particular, loss of dominant control in larger groups is a real possibility (Clutton-Brock 1998; Beekman et al. 2003). Distinguishing the alternatives will usually require more information on whether dominant control over the distribution of reproduction declines with increasing group size. One tactic would be to focus on species in which breeders suffer elevated mortality rates relative to nonbreeders or where total productivity declines with the proportion of group members that breed. Our model alone would predict a negative relationship between stable group size and the proportion of breeders in such cases.

Our study adds to a growing literature on the importance of resource inheritance in social evolution (Myles 1988; Field et al. 1999; Kokko and Johnstone 1999; Monnin and Peeters 1999; Monnin and Ratnieks 1999; Ragsdale 1999; Cant and Field 2001, 2005; Kokko et al. 2001; Clutton-Brock 2002; Shreeves and Field 2002; Buston 2003, 2004; Cant, English, et al. forthcoming; Cant, Llop, and Field forthcoming). To incorporate inheritance in models of this kind one must make some assumption about the protocol by which animals attain dominant status. We have assumed that individuals form a strict queue and move up in rank only when one of those ahead of them in the queue dies. This scheme fits some species well (e.g., primitively social wasps: Field et al. 1999; Cant and Field 2001, 2005; Sumner et al. 2002; vertebrates, Wiley and Rabenold 1984; East and Hofer 2001; Buston 2003, 2004). Alternative possibilities exist, however, which have only just started to be explored theoretically (Monnin and Ratnieks 1999; Cant and Johnstone 2000; Cant, Llop, and Field forthcoming). For example, in some termites, ants, mole-rats, and many primates, nonbreeders engage in vicious contests for any breeding vacancy that may arise (Pollock and Rissing 1985; Pusey and Packer 1987; Myles 1988; Clarke and Faulkes 1997; Thorne 1997). Even in the absence of a breeding vacancy, low rankers may jump the queue by attacking those of higher

rank (e.g., groove-billed anis, Vehrencamp et al. 1986; dunnocks, Davies 1992; hyenas, East and Hofer 2001; many primates, Walters and Seyfarth 1987). Variation in the protocol of inheritance and the costs of fighting can be expected to have important consequences for the stability of social hierarchies and the behavior expressed by individuals within them (Cant, English, et al. forthcoming; Cant, Llop, and Field forthcoming). Further studies of inheritance, both theoretical and empirical, provide important information on how future prospects influence current behavioral decisions and so improve our understanding of the major characteristics of long-lived social organisms.

**APPENDIX A**

**Probability of inheritance in queues and scrambles**

Consider a queue of  $b$  breeders with mortality rate  $m_B$  and  $s$  nonbreeders with mortality rate  $m_S$ . Total group size is  $n = b + s$ . We wish to obtain an expression for the probability that the lowest ranked individual (rank  $n$ ) survives to inherit the first available breeding position at rank  $b$ . From Expression 3, the probability that the rank  $n$  individual moves up one place is

$$p_{n \rightarrow n-1} = \frac{bm_B + (s-1)m_S}{bm_B + sm_S}$$

Once at rank  $n - 1$ , its probability of moving up another place to rank  $n - 2$  is

$$p_{n \rightarrow n-1} = \frac{bm_B + (s-2)m_S}{bm_B + (s-1)m_S}$$

and so on. The probability of surviving to move from rank  $n$  to rank  $b$  is therefore given by

$$\begin{aligned}
 p_{n \rightarrow b} &= [p_{n \rightarrow n-1}] \cdot [p_{n-1 \rightarrow n-2}] \cdot [p_{n-2 \rightarrow n-3}] \cdots [p_{b+1 \rightarrow b}] \\
 &= \left[ \frac{bm_B + (s-1)m_S}{bm_B + sm_S} \right] \cdot \left[ \frac{bm_B + (s-2)m_S}{bm_B + (s-1)m_S} \right] \\
 &\quad \cdot \left[ \frac{bm_B + (s-3)m_S}{bm_B + (s-2)m_S} \right] \cdots \left[ \frac{bm_B}{bm_B + m_S} \right] \\
 &= \left[ \frac{bm_B}{bm_B + sm_S} \right].
 \end{aligned}
 \tag{A1}$$

Substituting  $qn$  and  $(1 - q)n$  for  $b$  and  $s$ , respectively, yields Equation 8 in the text.

It is interesting to compare Equation 8 with a very different protocol of inheritance in which nonbreeders compete on equal terms for each breeding position that arises. In this case the probability of inheritance for a randomly selected nonbreeder is given by the following recursion relation:

$$p_{n \rightarrow b} = \left[ \frac{(s-1)m_S}{bm_B + sm_S} \right] p_{n \rightarrow b} + \left[ \frac{bm_B}{bm_B + sm_S} \right] \left[ \frac{1}{s} + \frac{s-1}{s} p_{n \rightarrow b} \right].
 \tag{A2}$$

This expression can be understood as follows. There are 3 possible events that can be associated with the first death of a group member. The first possibility is that the focal nonbreeder dies first, in which case its probability of inheritance is zero, so we do not need to include this possibility in our expression for  $p_{n \rightarrow b}$ . With probability  $(s - 1)m_S / (bm_B + sm)$  one of the other  $(s - 1)$  nonbreeders is the first to die, in which case no breeding vacancy arises and the focal individual's probability of inheritance remains equal to  $p_{n \rightarrow b}$ . Finally, with probability  $bm_B / (bm_B + sm_S)$ , the first individual in the group to die is a breeder, in which case the focal nonbreeder

can inherit the position (with probability  $1/s$ ) or not (with probability  $(s - 1)/s$ ); in the latter case, its probability of inheritance reverts to  $p_{n \rightarrow b}$ .

Solving the recursion equation A2 for  $p_{n \rightarrow b}$  yields

$$p_{n \rightarrow b} = \left[ \frac{bm_B}{bm_B + sm_S} \right],$$

which is identical to the probability of inheritance in the strict queue. This means that all our results concerning stable group size can be generalized to systems in which nonbreeders compete in a random scramble competition for each breeding vacancy that arises.

**APPENDIX B**

**The sign of  $\partial n^* / \partial q$**

Where  $x$  is sufficiently large or  $m_S$  sufficiently small, groups may stabilize in a region where  $\partial G / \partial n^* > 0$ , that is, at a size smaller than the most productive size (see Figure 1). Thus, in some cases the term  $\partial G(q, n^*) / \partial n^*$  in the denominator of Equation 13

$$A \left( Ax - \frac{\partial G(q, n^*(q))}{\partial n^*} \right) \tag{B1}$$

can be positive. Does this mean that Term B1 can sometimes be negative?

Let  $W_j(n^* - 1)$  and  $W_j(n^*)$  denote the payoffs of the second-to-last and last recruits to a stable group, respectively. Because  $n^*$  is defined as the stable group size,  $W_j(n^* - 1)$  must equal or exceed  $W_j(n^*)$ . Using Equation 9 we have

$$\frac{G_{n^*-1}}{(n^* - 1)(q(m_B - m_S) + m_S)} \geq \frac{G_{n^*}}{(n^*)(q(m_B - m_S) + m_S)}$$

or

$$\frac{n^*}{(n^* - 1)} \geq \frac{G_{n^*}}{G_{n^*-1}}$$

Substituting our expression for  $n^*$  (Expression 11 in the text) into the above yields, after simplification,

$$\frac{G_{n^*-1}}{G_{n^*} - Ax} \geq 1$$

or

$$Ax \geq G_{n^*} - G_{n^*-1}. \tag{B2}$$

Inequality B2 must hold, given our definition of stable group size. Taking  $G_{n^*} - G_{n^*-1}$  as a good approximation of the slope  $\partial G / \partial n^*$ , Inequality B2 implies that Inequality B1 is always nonnegative. This means that the predictions concerning the sign of the relationship  $\partial n^* / \partial q$  are valid regardless of whether groups stabilize in a region of increasing or decreasing productivity.

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