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Reproductive Skew in Multimember Groups

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ABSTRACT: Cooperative societies vary in the extent to which reproduction is skewed toward one or a few socially dominant animals. Many recent models attempt to explain this variation on the basis that a dominant who benefits from the presence of subordinates may offer them incentives, in the form of reproductive opportunities, to remain in the group. While most societies contain multiple members, however, these models have considered only the relationship between a dominant and a single subordinate or have assumed that all subordinates are identical. We develop an incentive-based evolutionary stable strategy model of reproductive skew in three-member groups, in which subordinates may vary in their opportunities for independent reproduction, their contribution to group productivity, and in their relatedness both to the dominant and to one another. Our model demonstrates that the conclusions of two-member models cannot all be generalized to larger groups. For example, relatedness among group members can influence whether or not the dominant does best to offer staying incentives to subordinates in a three-member, but not a two-member, group. Both the degree of skew and group stability depend on the relatedness between subordinates as well as on the relatedness of each to the dominant, and the incentives that each individual subordinate receives are influenced by the traits of the other. Whether such effects increase or decrease skew and group stability depends crucially on whether a third group member increases group productivity to a greater or lesser extent than the first.

Keywords: reproductive skew, cooperative breeding, relatedness, animal societies.

Cooperatively breeding groups may contain one reproductive individual or many. “Reproductive skew” is the term used to describe this variation. Groups in which a single breeder monopolizes reproduction are described as having high reproductive skew, whereas low skew groups are those in which all or most members breed. Much recent discussion of reproductive skew is based on the idea that dominants benefit from the presence of subordinates and may therefore offer them reproductive opportunities as an incentive to keep them in the group (Vehrencamp 1979; Emlen 1982; Stacey 1982; see Cant 1998; Clutton-Brock 1998; Reeve et al. 1998 for alternative approaches). Vehrencamp (1979, 1983*a*, 1983*b*) and Stacey (1982) were the first to analyze formally the division of reproduction in this way. In particular, Vehrencamp (1979, 1983*a*, 1983*b*) explicitly determined the magnitude of reproductive “staying incentives” that must be offered to subordinates, given that they have some probability of success should they choose to disperse and breed independently but will contribute to the productivity of the group should they remain. Her approach has subsequently been extended by Reeve and Ratnieks (1993), who consider the possibility of subordinates fighting for exclusive control of the group’s resources and determine the magnitude of the peace incentives that the dominant must offer to prevent this. Further elaborations include the analysis of asymmetries in relatedness between dominant and subordinate (Reeve and Keller 1995, 1996) and of competitive “bidding” between rival dominants for a subordinate’s help (Reeve 1998).

Despite the rapid development of skew theory, however, attention has focused almost entirely on the division of reproduction between the dominant individual, on the one hand, and the subordinate members of the group, on the other. The partitioning of reproduction among different subordinates has been virtually ignored: Vehrencamp’s (1983*a*, 1983*b*) analyses assumed that all subordinates in a group were identical and, thus, obtained equal shares of reproduction, while more recent analyses have been restricted to two-member groups in which there is only a single subordinate (Reeve and Ratnieks 1993; Reeve and Keller 1995, 1996; Reeve 1998). The best attempts to test the predictions of incentive-based models of skew empir-

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ically in larger groups have therefore had to adopt one of two unsatisfactory approaches. On the one hand, they may employ various simple indices to summarize the overall level of skew in different groups (e.g., Keller and Vargo 1993; Pamilo and Crozier 1996) and look for relationships with mean group relatedness or overall productivity, sacrificing much information about variation among subordinates (e.g., Reeve and Keller 1995; Jamieson 1997). On the other hand, they may treat dyadic interactions between a dominant and each of her subordinates as independent (see, e.g., Field et al. 1998).

Here, we address this neglected issue by considering the partitioning of reproduction among individuals in a group comprising a dominant and two subordinates who may differ in their opportunity for independent breeding, in their contribution to group productivity, and in their relatedness to the dominant (as in previous incentive-based models of skew, we assume that the dominant has complete control over reproduction and that the subordinates may freely choose to leave or join the group). We derive the conditions for group stability and consider how the evolutionarily stable level of skew and pattern of reproduction varies with differences in the attributes of each subordinate.

An Evolutionary Stable Strategy Model of Reproductive Skew in Three-Member Groups

We consider the distribution of reproduction in an association of three individuals, referred to as Alpha, Beta, and Gamma. Individual Alpha is the dominant member of the group, while Beta and Gamma are equally ranked subordinates. Dominance implies complete control over the reproductive opportunities allocated to both subordinates, whose only decision is whether to remain or leave the association, each individual making an independent choice (so that Beta has no direct influence over the reproductive opportunities allocated to Gamma and vice versa). The model thus corresponds to the "monarchical" three-player game suggested by Reeve and Ratnieks (1993) or to Vehrencamp's (1983*a*) model IIB, in which subordinates leave the group individually (although, unlike Vehrencamp, we allow for differences between the two subordinates). We are concerned only with the "staying incentive" of Reeve and Ratnieks (1993) and will not consider their "peace incentive."

The amount of reproduction yielded to a subordinate will depend on its prospects for successful reproduction if it were to leave the group (i.e., the severity of ecological constraints) and on the productivity advantages of association. To quantify these factors, we must specify a number of parameters: x_β denotes the expected reproductive success Beta would gain by leaving the group, relative to the expected reproductive success of Alpha (the established dominant individual) in the absence of any subordinate helpers, and x_γ denotes the corresponding value for Gamma. The parameters k_β and k_γ denote the expected reproductive success of a group comprising Alpha and either Beta or Gamma, respectively, relative to the expected reproductive success gained by Alpha in the absence of any helpers. The parameter k_2 denotes the expected reproductive success of a three-member group comprising Alpha and both subordinates, again relative to the expected reproductive success of Alpha alone. We assume that $k_2 > \max\{k_\beta, k_\gamma\}$, that is, total group reproduction is greater in an association with two subordinates than in an association with one. The degrees of relatedness (assumed in all cases to be symmetrical) between the members of the group are denoted $r_{\alpha\beta}$, $r_{\alpha\gamma}$, and $r_{\beta\gamma}$.

Our aims are to calculate the proportion of overall direct reproduction each individual obtains in a stable three-member association (denoted p_α, p_β, and p_γ, respectively, where $p_\alpha + p_\beta + p_\gamma = 1$) and to determine the conditions under which such a group is stable.

Solving the Model

As stated above, we assume that the dominant individual has at all times complete control over the amount of reproduction allocated to each subordinate. The only decision open to individuals Beta and Gamma is whether to remain or to leave the association (each individual making an independent decision). In a stable three-member group, under these circumstances, the amount of reproduction allocated to each subordinate must give it sufficient incentive to remain. At the same time, the dominant will allocate no more reproduction to either subordinate than is sufficient for this purpose.

To determine what reproductive incentives are necessary, and whether the dominant will yield them, we make use of Hamilton's (1964) rule: contingent on the behavior of others, each individual will behave so as to maximize its own inclusive fitness. In this case, inclusive fitness is given by the sum of an individual's own reproduction, plus the reproduction of the other two individuals, each of the latter two numbers being devalued according to the degrees of relatedness between the group members. The value of this sum following a particular decision will be referred to as the fitness consequence of that decision.

For individual Beta, the fitness consequence of staying in a stable group, w^β_{stay}, is given by

$$w^\beta_{\text{stay}} = k_2(r_{\alpha\beta}p_\alpha + p_\beta + r_{\beta\gamma}p_\gamma). \tag{1}$$

What would happen if Beta were to leave? We assume that both Alpha and Gamma would have the opportunity to respond to the departure, Alpha (who would retain control over reproduction) by readjusting the amount of reproduction allocated to Gamma, and the latter perhaps (following this readjustment) by leaving. We can then make use of Reeve and Ratnieks's (1993) results to determine the anticipated outcome of the interaction between the two remaining group members: if $x \leq r_{\alpha\gamma}(k_\gamma - 1)$, then the remaining subordinate would stay in the two-member group, without being allocated any reproduction. In this case, the fitness consequence for Beta of leaving is given by

$$w^{\beta}_{\text{leave}} = k_\gamma r_{\alpha\beta} + x_\beta. \tag{2}$$

If $r_{\alpha\gamma}(k_\gamma - 1) < x < k_\gamma - 1$, then the other subordinate would remain in the two-member group, obtaining a proportion of reproduction, $\hat{p}_\gamma$, given by

$$\hat{p}_\gamma = \frac{x_\gamma - r_{\alpha\gamma}(k_\gamma - 1)}{k_\gamma(1 - r_{\alpha\gamma})}, \tag{3}$$

and the fitness consequence for Beta of leaving is then given by

$$w^{\beta}_{\text{leave}} = k_\gamma r_{\alpha\beta}(1 - \hat{p}_\gamma) + x_\beta + k_\gamma r_{\beta\gamma}\hat{p}_\gamma. \tag{4}$$

Finally, if $k_\gamma - 1 \leq x$, then the remaining subordinate would leave, following Beta's departure, and the fitness consequence for Beta of leaving is given by

$$w^{\beta}_{\text{leave}} = r_{\alpha\beta} + x_\beta + r_{\beta\gamma}x_\gamma. \tag{5}$$

An equivalent procedure to this can be used to determine w^{γ}_{stay} and $w^{\gamma}_{\text{leave}}$.

Having obtained expressions for w^{β}_{stay}, w^{β}_{leave}, w^{γ}_{stay}, and $w^{\gamma}_{\text{leave}}$, we can then determine p_β and p_γ, the shares of direct reproduction that Beta and Gamma obtain in a stable three-member group, by solving the simultaneous equations

$$w^{\beta}_{\text{stay}} = w^{\beta}_{\text{leave}}, \tag{6a}$$

$$w^{\gamma}_{\text{stay}} = w^{\gamma}_{\text{leave}}, \tag{6b}$$

which imply that each subordinate receives sufficient incentive to remain, but no more. A problem arises if these equations yield negative values for either p_β or p_γ, indicating that one or both subordinates will remain without any share of direct reproduction. In such cases, the value of p_β when Gamma will remain without direct reproduction can be obtained by solving the equation

$$w^{\beta}_{\text{stay}}\Big|_{p_\gamma=0} = w^{\beta}_{\text{leave}}, \tag{7}$$

while the value of p_γ when Beta will remain without direct reproduction is given by

$$w^{\gamma}_{\text{stay}}\Big|_{p_\beta=0} = w^{\gamma}_{\text{leave}}. \tag{8}$$

The final step is to determine whether a three-member group is stable. In other words, assuming that one or both subordinates require an incentive to remain, we must determine whether the dominant gains by allocating the staying incentives p_β and p_γ, whether it would do better to retain only one subordinate, or neither. The fitness consequence for the dominant of yielding both incentives, $w^{\alpha}_{\beta+/\gamma+}$, is given by

$$w^{\alpha}_{\beta+/\gamma+} = k_2(p_\alpha + r_{\alpha\beta}p_\beta + r_{\alpha\gamma}p_\gamma). \tag{9}$$

The fitness consequence for the dominant of withholding both incentives (thus causing both subordinates to leave the association), denoted $w^{\alpha}_{\beta-/\gamma-}$, is given by

$$w^{\alpha}_{\beta-/\gamma-} = 1 + r_{\alpha\beta}x_\beta + r_{\alpha\gamma}x_\gamma. \tag{10}$$

To calculate the fitness consequence for the dominant of withholding the staying incentive from one subordinate, we can again make use of Reeve and Ratnieks's (1993) results. Suppose Alpha withholds any incentive from Beta, and the latter leaves; the outcome of the ensuing interaction between Alpha and Gamma can be determined as described above. If $x \leq r_{\alpha\gamma}(k_\gamma - 1)$, then Gamma will remain without any direct reproductive opportunity. The fitness consequence for the dominant, $w^{\alpha}_{\beta-/\gamma+}$, is then given by

$$w^{\alpha}_{\beta-/\gamma+} = k_\gamma + r_{\alpha\beta}x_\beta. \tag{11}$$

If $r_{\gamma\alpha}(k_\gamma - 1) < x$, then Gamma requires a staying incentive $\hat{p}_\gamma$ to stay, as defined in equation (3). Consequently, $w^{\alpha}_{\beta-/\gamma+}$ is given by

$$w^{\alpha}_{\beta-/\gamma+} = k_\gamma(1 - \hat{p}_\gamma) + r_{\alpha\beta}x_\beta + r_{\alpha\gamma}k_\gamma\hat{p}_\gamma. \tag{12}$$

An equivalent calculation yields the value $w^{\alpha}_{\beta+/\gamma-}$. The requirement for the three-member group to be stable is then

$$w^{\alpha}_{\beta+/\gamma+} > \max[w^{\alpha}_{\beta-/\gamma+}, w^{\alpha}_{\beta+/\gamma-}, w^{\alpha}_{\beta-/\gamma-}]. \qquad (13)$$

Equations (1)–(13) can be used to determine whether a three-member group is stable and, if so, what incentives must be offered to subordinates at equilibrium. Unfortunately, the effects of the model's various parameters on stability and incentive size cannot be summarized in a single analytical expression. The reason for this is that the model yields a different solution according to whether a two-member association between the dominant and each of the subordinates would prove unstable, stable with incentives, or stable without incentives. Since there are three possibilities regarding association with each of Beta and Gamma, this yields nine different solutions, each valid over only a part of the parameter space of the model. Moreover, each solution comprises several different expressions, specifying stability conditions and the division of reproduction when both subordinates must be offered an incentive to remain and when only Beta or only Gamma requires an incentive (together with the conditions for which each of these cases applies).

In light of the above, we will not attempt to summarize in full the outcome of the model. Instead, we illustrate the effects of the various parameters graphically in the next section.

Results

We start by considering the effects of differences in relatedness among group members, in cases where both subordinates are otherwise identical, that is, have the same opportunity for independent breeding and make the same contribution to group productivity (so that $x_{\alpha} = x_{\beta} = x$ and $k_{\alpha} = k_{\beta} = k$). Three subsections are devoted to the effects of relatedness: the first deals with the overall degree of kinship in a group of homogeneous relatedness, the second considers what happens when subordinates are more or less closely related to each other than to the dominant, and the third looks at groups in which one subordinate is more closely related to the dominant than is the other. Having examined relatedness in detail, we then move on to examine the consequences of differences between Beta and Gamma in the opportunity for independent breeding and in contribution to productivity.

Two related factors that exert a major influence on the outcome of the model are the stability of a two-member group under the given conditions and the contribution that the presence of a second helper makes to group productivity relative to that of the first (i.e., the shape of the relationship between group productivity and group size). The former is important because it influences the fitness consequences of leaving for both subordinates in a three-member association (the consequences of Beta leaving, e.g., depend on whether Gamma would then remain in a two-member association with Alpha). The latter is important because it determines the relative size of the staying incentives that pairs of helpers and lone subordinates require. For instance, when a three-member group is much more productive than a two-member association (in other words when group productivity is an accelerating, i.e., concave up, function of group size), a dominant need not offer much in the way of staying incentives to either of a pair of helpers because each gains considerable indirect fitness by remaining in the association. In turn, incentive sizes determine whether the dominant stands to gain by sacrificing sufficient reproduction to retain two helpers. Throughout the analysis that follows, we will make repeated reference to these two key factors.

The graphs presented below were all obtained by numerical solution of equations (1)–(13), using Mathematica (Wolfram Research 1991). The standard plotting function of this program was used to generate the curves; in each case, the solution was initially evaluated at 100 points equally spaced over the interval shown, after which the plotting algorithm chooses further sampling points in an attempt to generate a smooth curve (the maximum subdivision of the original interval during this process was set at a factor of 20, yielding an upper limit to resolution of 1/2,000 of the plotting range). The parameter values for the graphs were chosen in an attempt to illustrate the widest possible range of effects that the model produces.

The Effects of Overall Relatedness

We begin by focusing on the case of a group of homogeneous relatedness, where $r_{\alpha\beta} = r_{\alpha\gamma} = r_{\beta\gamma} = r$. Figure 1 shows the level of reproductive skew in a stable three-member group, as a function of the expected fitness that would be gained by a subordinate who left the group to breed independently (x), for several different values of k_2 (the productivity of a three-member group relative to that of a lone breeder).

In figure 1, graph *A* shows results for a group of unrelated individuals (in which each subordinate requires a staying incentive of value x), graph *B* for a group in which the coefficient of relatedness between all individuals is 0.5 (e.g., a mother and two full-sib daughters or three full sibs). Skew (both here and throughout the article) is measured by Pamilo and Crozier's (1996) index S:

$$S = (N_{\mathrm{T}} - Q_{\mathrm{E}})/(N_{\mathrm{T}} - 1), \qquad (14)$$

where N_{T} is the total number of potential breeders and Q_{E} is the "effective number" of breeders, defined as

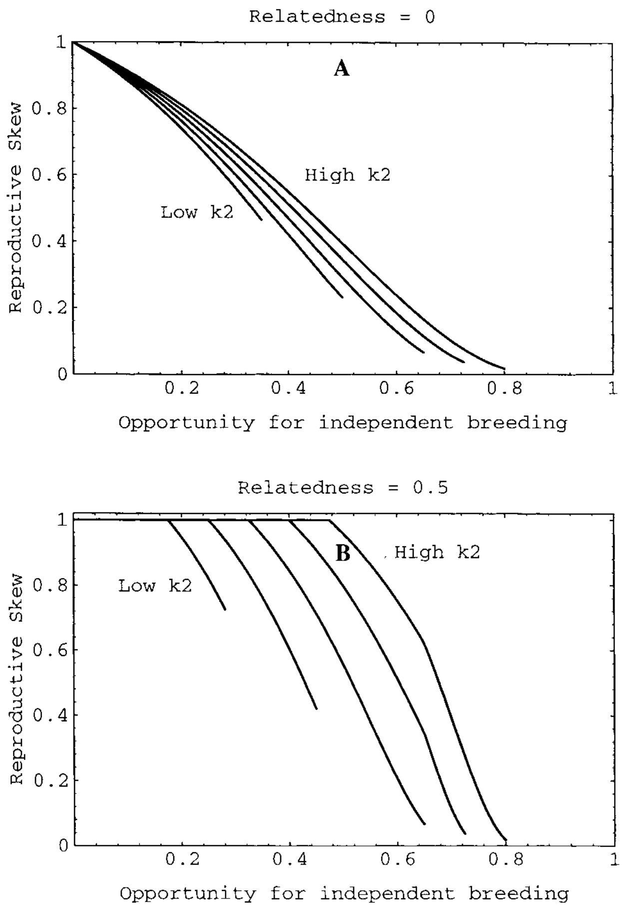

Figure 1: Reproductive skew in a three-member group (measured by Pamilo and Crozier's [1996] index *S*, defined in the main text), as a function of the expected fitness that would be gained by a subordinate who left the group to breed independently ($x_\beta = x_\gamma$), for several different values of k_2 (the productivity of a three-member group relative to that of a lone breeder). Graph *A*, Results for a group of unrelated individuals. Graph *B*, Results for a group in which the coefficient of relatedness between all individuals is 0.5. In both cases, curves are plotted over the range of parameter values for which a three-member group is stable, and successively lower curves correspond to successively lower values of k_2: 2.6, 2.45, 2.3, 2.15, and 2. In all cases, $k_\beta = k_\gamma = 1.65$.

$Q_E = 1/p_i^2$, where p_i is the share of direct reproduction obtained by the *i*th breeder.

The figure reveals that, when subordinates have a greater opportunity to breed independently (i.e., when ecological constraints are weaker), skew is predicted to decrease and a three-member group is less likely to be stable (just as in the "two-queen" model of Reeve and Ratnieks 1993). Furthermore, the smaller the contribution that a second helper makes to group productivity, the lower the skew (and the less likely a three-member group is to be stable). The latter effect is more marked when group members are related; skew also tends to be higher among relatives than among nonrelatives for any given level of contribution.

Figure 2 illustrates the effects of relatedness in more detail. As in the two-queen model, skew is predicted to be greater when group members are more closely related to each other. In contrast to the two-queen case, however, relatedness can also influence group stability (provided that a two-member group is stable and a second helper contributes less to group productivity than the first). When k_2 is large enough, that is, when a second helper makes a big enough contribution to group productivity, a three-member group will prove stable regardless of relatedness. Equally, when k_2 is small enough, such a group will prove unstable regardless of relatedness. Between these extremes, however, is a range in which a three-member group proves stable for either high or low levels of relatedness but not for intermediate values of *r*.

Figure 3 demonstrates why group stability is most likely at extreme levels of relatedness (either low or high). Graph *A* shows (for a sample case in which a two-member group is stable and a second helper contributes less than the first) the absolute amount of direct reproduction that must be allocated to subordinates in a two-member and in a three-member group as a function of *r*. The difference between the two, devalued according to the relatedness between dominant and subordinates, represents the cost to the dominant of retaining a second helper (the devaluation is necessary because the cost of yielding direct reproduction to a subordinate is reduced if it is a close relative). Graph

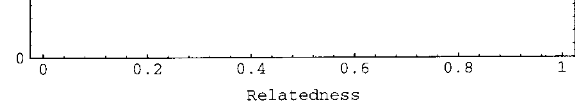

Figure 2: Reproductive skew in a three-member group (measured by Pamilo and Crozier's [1996] index *S*, defined in the main text), as a function of the coefficient of relatedness between group members (*r*), for several different values of k_2 (the productivity of a three-member group relative to that of a lone breeder). Curves are plotted over the range of parameter values for which a three-member group is stable, and successively lower curves correspond to successively lower values of k_2: 2.5, 2.3, 2.1, and 2.075. In all cases, $k_\beta = k_\gamma = 1.65$ and $x_\beta = x_\gamma = 0.4$.

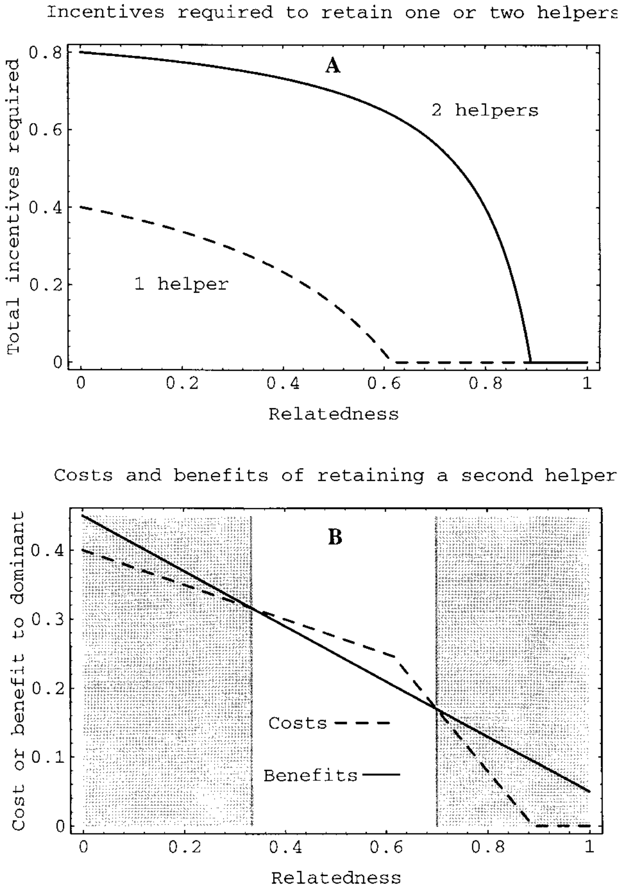

Figure 3: Graph *A*, The absolute magnitude of the total incentives required to retain either one (*dashed line*) or two (*solid line*) helpers, as a function of the coefficient of relatedness between group members (r), assuming that $k_\beta = k_\gamma = 1.65$, $k_2 = 2.1$, and $x_\beta = x_\gamma = 0.4$. The difference between the two curves thus represents the extra incentive required to retain a second helper (in addition to the first). Graph *B* shows the fitness cost to the dominant of yielding this additional incentive (*dashed line*) as well as the fitness benefit to be gained by retaining a second helper (*solid line*). A three-member group is stable if and only if the cost to the dominant of retaining two subordinates is less than the benefit it stands to gain by doing so. The regions where this is the case ($r < 0.33$ and $r > 0.70$) have been shaded in the graph.

B shows this cost (dotted line) together with the benefit that the dominant gains (solid line). The latter also declines with relatedness because the enhanced productivity of a group containing two helpers is increasingly offset by the loss of the reproductive success that the second helper might have obtained by breeding independently. When the group members are unrelated, this loss of reproduction does not matter to the dominant, but as r increases, it assumes ever greater significance.

Initially, as r increases from zero, the benefit declines more rapidly than the cost. Consequently, although a three-member group is stable for $r = 0$, it ceases to be so above some critical level of relatedness. However, once the point is reached where a single subordinate will remain in the group without being allocated any reproduction, the decline in the cost of retaining a second helper becomes more rapid than the decline in benefit (because the reproductive incentives that must be offered in a three-member group continue to drop, while incentive size in a two-member group remains fixed at zero). A new threshold level of relatedness is thus reached above which benefits exceed costs, and a three-member group again proves stable.

The Effects of Intersubordinate Relatedness

As well as investigating the effects of overall relatedness, we can also consider situations in which the coefficient of relatedness between the two subordinates Beta and Gamma is less than or greater than their degree of relatedness to the dominant Alpha. Figure 4, for example, shows (for a sample case in which a two-member group is stable) the evolutionary stable strategy (ESS) level of reproductive skew as a function of intersubordinate relatedness ($r_{\beta\gamma}$), for three different values of k_2 (the productivity of a three-member group relative to that of a lone breeder). In both graphs, the dot-dashed line was calculated using a high value of k_2, which implies that a second helper contributes more to group productivity than the first, and the dotted line using a low value of k_2, which implies that a second helper contributes less than the first. The solid line corresponds to the case in which successive helpers make the same contribution. Graph *A* gives results for a group in which the relatedness of subordinates to the dominant equals 0.5, and graph *B* for a group in which it equals 0.25. Note that, in both cases, $r_{\beta\gamma}$ cannot drop below the product of $r_{\alpha\beta}$ and $r_{\alpha\gamma}$ (0.25 in graph *A*, 0.0625 in graph *B*) since the fact that both subordinates are related to the dominant implies that they are to some degree related to each other.

Both graphs demonstrate that if a second helper contributes more than the first, then skew tends to be lower when subordinates are closely related to one another (indicating that the dominant must yield greater incentives under these conditions). Conversely, if a second helper contributes less than the first, skew tends to be higher when subordinates are more closely related to each other (indicating that the dominant need only yield smaller incentives). Both effects are more strongly marked when the subordinates are more closely related to the dominant.

The effects of intersubordinate relatedness on the size of the incentives that the dominant must give out can also influence group stability. The upper graph shows that, for

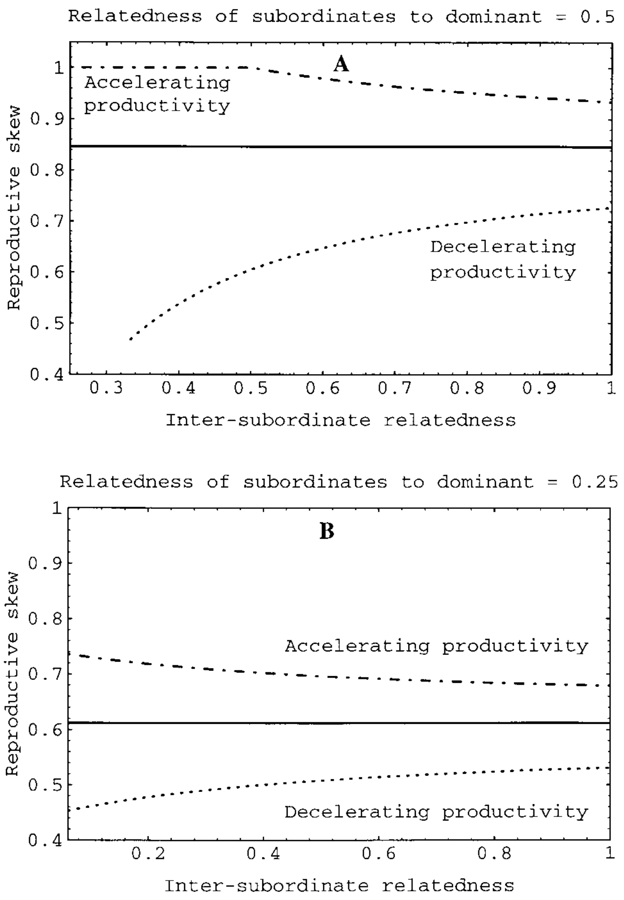

Figure 4: Reproductive skew in a three-member group (measured by Pamilo and Crozier's [1996] index S, defined in the main text), as a function of the coefficient of relatedness between subordinates ($r_{\beta\gamma}$), for several different values of k_2 (the productivity of a three-member group relative to that of a lone breeder). Curves are plotted over the range of parameter values for which a three-member group is stable. Graph *A*, Results for a group in which the relatedness of each subordinate to the dominant equals 0.5. Graph *B*, Results for a group in which the relatedness of each subordinate to the dominant equals 0.25. In all cases, $k_\beta = k_\gamma = 1.65$ and $x_\beta = x_\gamma = 0.4$. *Solid line* represents results for $k_2 = 2.3$ (implying that a second helper contributes the same amount to group productivity as the first); *dotted line*, results for $k_2 = 2.15$ (implying that a second helper contributes less than the first); and *dot-dashed line*, results for $k_2 = 2.45$ (implying that a second helper contributes more than the first).

the case where a second helper contributes less than the first, a drop in intersubordinate relatedness can lead to the breaking up of a group that would otherwise have been stable (this is indicated by the fact that the dotted curve does not continue below $r_{\beta\gamma} = 1/3$). For the parameter values used in this case, a group comprising a dominant mother and two subordinate full-sib daughters (in which $r_{\alpha\beta} = r_{\alpha\gamma} = r_{\beta\gamma} = 0.5$) will prove stable, while a group comprising a mother and two half-sib daughters who have different fathers (in which $r_{\alpha\beta} = r_{\alpha\gamma} = 0.5$ and $r_{\beta\gamma} = 0.25$) will not.

Why should the level of intersubordinate relatedness affect the size of the incentives that the dominant must offer to retain both helpers? Consider the case in which a second helper contributes less than the first to group productivity. Under these circumstances, a subordinate in a three-member group will require a larger staying incentive than a subordinate in a two-member group (since the latter gains a greater indirect fitness benefit from remaining). Consequently, the departure of one subordinate (say Beta) from a three-member group will result in a decrease in the size of incentive that the other subordinate (Gamma) receives and a corresponding increase in the direct reproductive share of the dominant (Alpha). If Beta is more closely related to Gamma than she is to Alpha, then this transfer of reproduction will have a negative impact on her fitness; conversely, if she is more closely related to Alpha than to Gamma, then it will have a positive impact. The more closely related the two subordinates are, the more deleterious (or the less beneficial) the impact of the change is on the departing subordinate's inclusive fitness. As a result, when $r_{\beta\gamma}$ is high, less of an incentive is needed to induce each subordinate to remain because the consequences of leaving are worse. Skew thus increases with intersubordinate relatedness. The reverse will be true when a second helper contributes more to group productivity than the first.

Variation in the Relatedness of the Dominant to Different Subordinates

Finally, we can consider groups in which one subordinate is more closely related to the dominant than is the other. Figure 5 shows the share of total group productivity allocated by the dominant Alpha to both Beta (solid line) and Gamma (dashed line), as a function of the relatedness between Alpha and Beta, assuming that Gamma is unrelated to either. In the upper graph, a second helper contributes less than the first to group productivity, while in the lower graph a second helper contributes more than the first. In both cases, a two-member group involving either subordinate is stable with incentives.

The figure reveals that the unrelated subordinate Gamma requires a larger staying incentive than Beta (who is closely related to the dominant). This is simply because Beta gains a greater indirect fitness benefit by staying to assist the dominant. On the one hand, the greater the value of $r_{\alpha\beta}$, the smaller Beta's incentive, regardless of whether a second helper contributes more or less than the first (though the effect is more marked in the former case). Gamma's incentive, on the other hand, is unaffected by

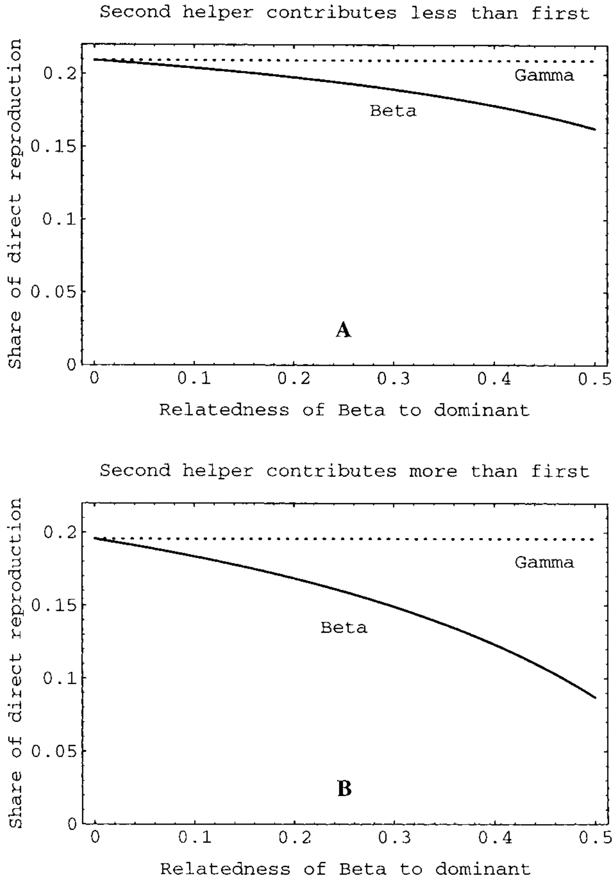

Figure 5: The proportion of total group productivity given as an incentive to Beta (*solid line*) and to Gamma (*dashed line*) as a function of the relatedness of Beta to Alpha ($r_{\alpha\beta}$), assuming that Gamma is unrelated to either. Graph *A*, Results for the case where a second helper contributes less to group productivity than the first ($k_2 = 2.15$). Graph *B*, Results for the case where a second helper contributes more than the first ($k_2 = 2.3$). Other parameter values are $k_\beta = k_\gamma = 1.6$ and $x_\beta = x_\gamma = 0.45$.

the coefficient of relatedness between Alpha and Beta (since she is unrelated to either).

Figure 6 shows the share of total group productivity allocated to Beta (solid line) and Gamma (dashed line), as a function of the relatedness between Alpha and Beta, assuming that the relatedness between Alpha and Gamma is fixed at 0.5 (note that the two subordinates are assumed to be related only through the dominant). In the upper graph, a second helper contributes less than the first to group productivity, while in the lower graph a second helper contributes more than the first. In both cases, a two-member group involving either subordinate is stable with incentives.

Once again, the subordinate that is less closely related to the dominant (in this case Beta) requires a larger staying incentive. The lower the value of $r_{\alpha\beta}$, the larger Beta's incentive, regardless of whether a second helper contributes more or less than the first, though the effect is more marked in the former case. In contrast with the previous figure, however, the proportion of reproduction allocated to Gamma is also influenced by the coefficient of relatedness between Alpha and Beta. When a second helper contributes less than the first to group productivity, Gamma's incentive increases with $r_{\alpha\beta}$. In other words, the more closely related Beta is to the dominant, the larger the incentive that Gamma receives. Conversely, when a second helper contributes more than the first to group productivity, Gamma's incentive decreases with $r_{\alpha\beta}$.

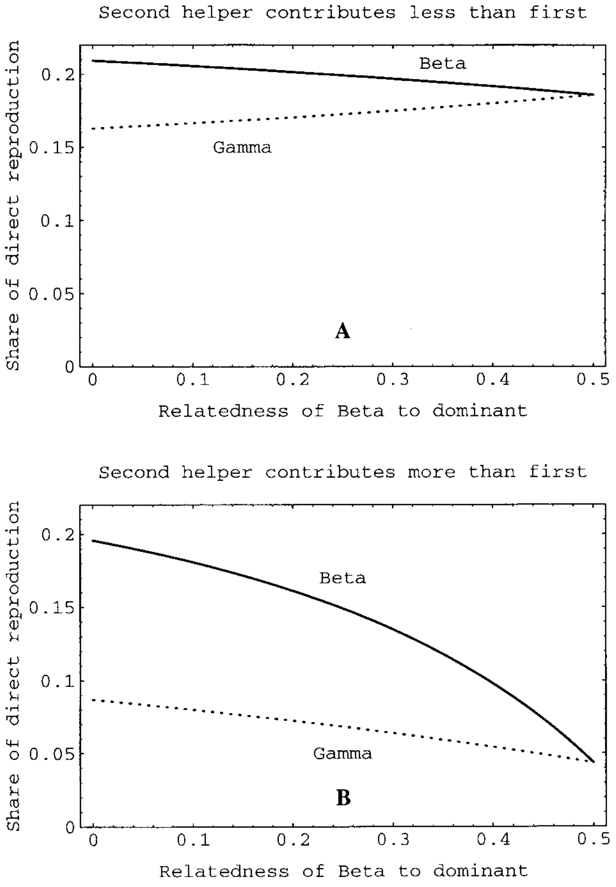

Figure 6: The proportion of total group productivity given as an incentive to Beta (*solid line*) and to Gamma (*dashed line*) as a function of the relatedness of Beta to the dominant ($r_{\alpha\beta}$), assuming that the relatedness of Gamma to the dominant ($r_{\alpha\gamma}$) is fixed at 0.5. Relatedness between the two subordinates ($r_{\beta\gamma}$) is assumed to equal the product of $r_{\alpha\beta}$ and $r_{\alpha\gamma}$, which implies that the two subordinates are related only through the dominant. Graph *A*, Results for the case where a second helper contributes less to group productivity than the first ($k_2 = 2.15$). Graph *B*, Results for the case where a second helper contributes more than the first ($k_2 = 2.3$). Other parameter values are $k_\beta = k_\gamma = 1.6$ and $x_\beta = x_\gamma = 0.45$.

The parameter $r_{\alpha\beta}$ exerts an influence on Gamma's incentive size in this case because Gamma is related to Alpha ($r_{\alpha\gamma} = 0.5$). Consequently, any increase in the relatedness between Alpha and Beta also entails an increase in the relatedness between Gamma and Beta. The consequences of the latter effect, however, depend on the relative contributions of successive helpers to group productivity (as outlined in the previous section). Consider the case in which a second helper contributes less than the first. Under these circumstances, a subordinate in a three-member group requires a larger staying incentive than a subordinate in a two-member group (since the latter gains a greater indirect fitness benefit from remaining). Consequently, Gamma's departure from the group would result in a decrease in the size of Beta's incentive and a corresponding increase in the direct reproductive share of the dominant (Alpha). The more closely related Gamma is to Beta, the more negative (or less positive) the impact of this transfer of reproduction (from Beta to Alpha) on Gamma's fitness. As a result, the greater the value of $r_{\beta\gamma}$, the smaller the staying incentive that Gamma requires because the consequences of leaving are worse. The reverse is true when a second helper contributes more than the first to group productivity (note that both effects also apply to Beta but are largely outweighed by the impact of $r_{\alpha\beta}$ on the indirect fitness benefits that Beta gains by contributing to the reproductive success of the dominant Alpha).

Differences between Subordinates in the Opportunity for Independent Breeding

Having examined the effects of differences in relatedness on the division of reproduction, we now turn to the consequences of other differences between subordinates. Figure 7 shows the share of direct reproduction granted to Beta (solid line) and to Gamma (dotted line) as a function of Gamma's opportunity for independent breeding (x_γ), assuming that Beta's opportunity (x_β) is fixed at 0.35 (in a group of homogeneous relatedness where $r_{\alpha\beta} = r_{\alpha\gamma} = r_{\beta\gamma} = 0.5$). Unsurprisingly, the greater Gamma's opportunity to breed independently, the larger the share of reproduction she receives as a staying incentive. Changes in x_γ, however, have no effect on the share of reproduction granted to Beta.

By contrast, when relatedness among group members is not homogeneous, Gamma's opportunity for independent breeding can influence the size of staying incentive that Beta requires. Figure 8 again shows the share of direct reproduction granted to Beta (solid line) and to Gamma (dotted line) as a function of Gamma's opportunity for independent breeding (x_γ), assuming that Beta's opportunity (x_β) is fixed. This time, however, the subordinates are assumed to be less closely related to each other than they are to the dominant. Specifically, $r_{\alpha\beta} = r_{\alpha\gamma} = 0.5$, while $r_{\beta\gamma} = 0.25$ (which corresponds, e.g., to a dominant mother with two subordinate half-sib daughters). In graph *A*, a second helper contributes less to group productivity than the first, while in graph *B* a second helper contributes more.

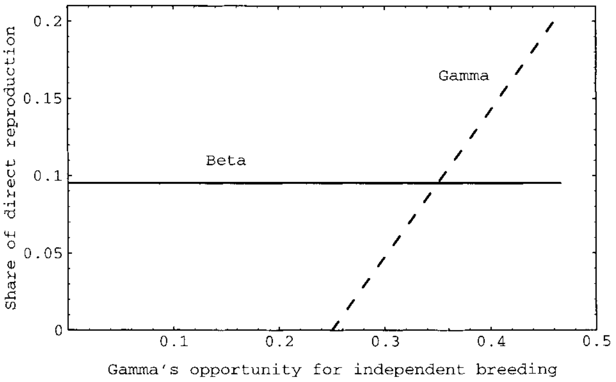

Figure 7: The proportion of total group productivity given as an incentive to Beta (*solid line*) and to Gamma (*dashed line*) when $r_{\alpha\beta} = r_{\alpha\gamma} = r_{\beta\gamma} = 0.5$, as a function of Gamma's opportunity for independent breeding (x_γ), assuming that Beta's opportunity (x_β) is fixed at 0.35. Other parameter values are $k_\beta = k_\gamma = 1.6$ and $k_2 = 2.1$ (which implies that a second helper contributes less to group productivity than the first). Curves are plotted over the range of values for which a three-member group is stable ($x_\gamma < 0.467$).

In graph *A*, an increase in x_γ not only results in Gamma receiving a larger share of direct reproduction but also leads to an increase in Beta's incentive, up to a point. By contrast, in graph *B*, Beta's incentive first decreases with x_γ, then levels out, and finally starts to increase again. What gives rise to these changes?

Consider, first, the case where a second helper contributes less to group productivity than the first (graph *A*). As x_γ increases from zero, a point is reached at which Gamma starts to receive increasingly large staying incentives in a three-member group, while still requiring none in a two-member group (because she makes a greater contribution to the latter, thus reaping a larger indirect benefit from helping the dominant). Since the two subordinates are less closely related to each other than to the dominant, this leads to a reduction in the inclusive fitness Beta gains by remaining in a three-member group (where Gamma receives an increasing share of reproduction) relative to that which she would gain by leaving (after which Gamma would not receive any incentive from the dominant). Consequently, she requires a larger staying incentive (the effect would be reversed if the two subordinates were more closely related to each other than they were to the dominant). Eventually, however, as x_γ increases, Gamma starts

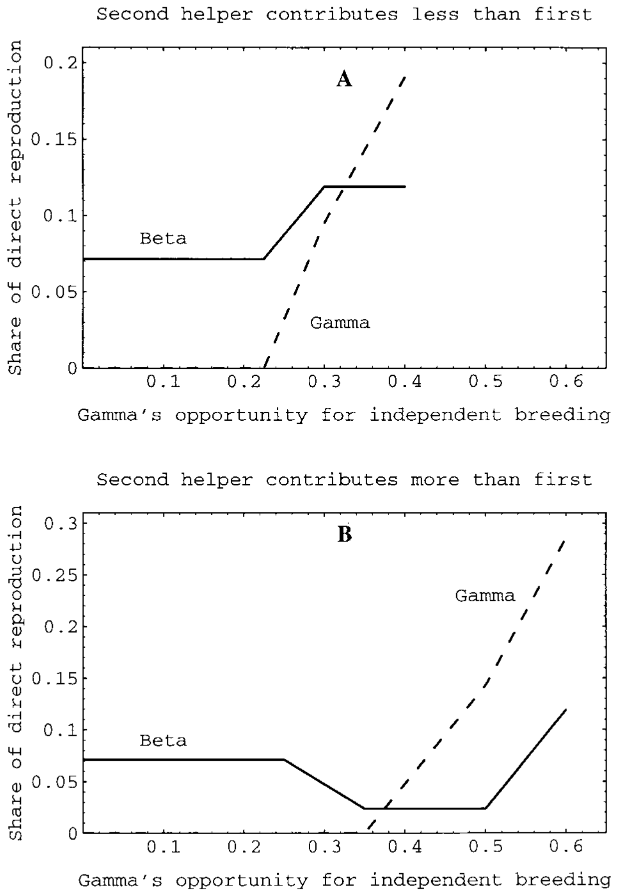

Figure 8: The proportion of total group productivity given as an incentive to Beta (*solid line*) and to Gamma (*dashed line*) when $r_{\alpha\beta} = r_{\alpha\gamma} = 0.5$ and $r_{\beta\gamma} = 0.25$, as a function of Gamma's opportunity for independent breeding (x_γ), assuming that Beta's opportunity (x_β) is fixed, at 0.35 in graph *A* and at 0.375 in graph *B*. In the former case, $k_\beta = k_\gamma = 1.6$ and $k_2 = 2.1$, implying that a second helper contributes less than the first, while in the latter, $k_\beta = k_\gamma = 1.5$ and $k_2 = 2.1$, implying that a second helper contributes more than the first. Curves are plotted over the range of values for which a three-member group is stable ($x_\gamma < 0.4$ in graph *A* and $x_\gamma < 0.6$ in graph *B*).

to require an incentive to remain in a two-member as well as a three-member group. Above this point, x_γ ceases to influence Beta's incentive size because any increase in the share of reproduction that Gamma requires in a three-member group is matched by an increase in the share she would receive in a two-member group.

When a second helper contributes more to group productivity than the first (graph *B*), the results are rather different. As x_γ increases from zero, Gamma first starts to require incentives in a two-member group, while still requiring none in a three-member group (to which she makes a greater contribution). This leads to a decrease in the inclusive fitness that Beta would gain by leaving relative to that which she gains by remaining in a three-member group and, thus, to a decrease in the staying incentive she requires. Once again, the effect would be reversed if the two subordinates were more closely related to each other than they were to the dominant. Once the point is reached where Gamma's incentive starts to increase with x_γ in a three-member as well as in a two-member group, however, the decrease in Beta's incentive size levels off. Finally, above the point at which a two-member association between Alpha and Gamma becomes unstable, Beta's staying incentive starts to increase with x_γ simply because the fitness consequences of her leaving are improved if Gamma is more likely to be successful when breeding independently.

Differences between Subordinates in Their Contribution to Group Productivity

Finally, we can consider the consequences of differences between subordinates in the contribution that they make to group productivity. Figure 9 shows the proportion of total group productivity given as an incentive to Beta (solid line) and to Gamma (dashed line), in a group of homogeneous relatedness ($r_{\alpha\beta} = r_{\alpha\gamma} = r_{\beta\gamma} = 0.5$), as a function of Gamma's contribution to group productivity ($k_\gamma - 1$), assuming that Beta's contribution is fixed at 0.6 (i.e., $k_\beta = 1.6$). In this case, each helper is assumed to make the same contribution in a three-member as in a two-member group (i.e., $k_2 = k_\gamma + 0.6$).

Unsurprisingly, the greater Gamma's contribution to

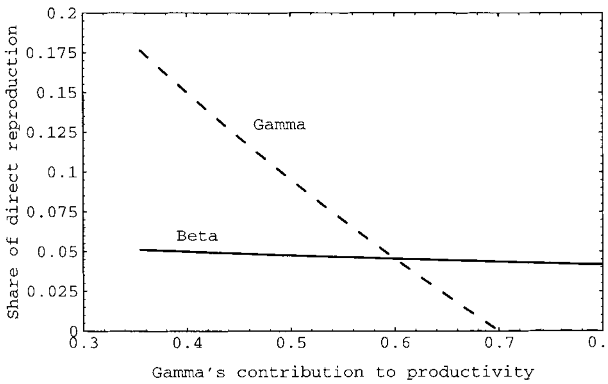

Figure 9: The proportion of total group productivity given as an incentive to Beta (*solid line*) and to Gamma (*dashed line*) when $r_{\alpha\beta} = r_{\alpha\gamma} = r_{\beta\gamma} = 0.5$, as a function of Gamma's contribution to group productivity ($k_\gamma - 1$), assuming that Beta's contribution is fixed at 0.6 (i.e., $k_\beta = 1.6$). We assume that $k_2 = k_\gamma + 0.6$, which implies that each helper makes the same contribution in a three-member as in a two-member group. Other parameter values are $x_\beta = x_\gamma = 0.35$.

group productivity, the smaller the share of direct reproduction that she requires as a staying incentive (because she gains a greater indirect fitness benefit from helping the dominant). In addition, there is a slight decrease in the share of reproduction that Beta requires. The latter effect simply reflects the fact that, when Gamma makes a larger contribution, total group productivity is enhanced, so that Beta will be satisfied with a smaller share.

More complex results are obtained when relatedness within a three-member group is not homogeneous. Figure 10 again shows the proportion of total group productivity, given as an incentive to Beta (solid line) and to Gamma (dashed line), as a function of Gamma's contribution to group productivity ($k_\gamma - 1$), assuming that Beta's contribution is fixed at 0.5 (i.e., $k_\beta = 1.5$), this time assuming that the two subordinates are less closely related to each other than they are to the dominant ($r_{\alpha\beta} = r_{\alpha\gamma} = 0.5$ and $r_{\beta\gamma} = 0.25$). In graph *A*, each helper makes less of a contribution in a three-member than in a two-member group. In graph *B*, by contrast, each helper makes more of a contribution in a three-member group.

Consider the case where each helper makes proportionately less of a contribution in a three-member group (graph *A*). As Gamma's contribution to productivity increases, the staying incentive she requires also declines, but it does so more rapidly in a two-member than in a three-member group (since the contributions of each helper is of more significance in the former case). Since Beta is less closely related to Gamma than to the dominant, the resulting decrease in Gamma's share of reproduction in a two-member relative to a three-member group leads to an increase in Beta's inclusive fitness if she leaves relative to her fitness if she stays. The result is a slight increase in the staying incentive that Beta requires to remain in a three-member association. However, once the point is reached at which Gamma will remain in a two-member group without incentives, this effect is reversed. Gamma's share of reproduction in a three-member group continues to drop, so that Beta's inclusive fitness in such an association, relative to the fitness she would gain by leaving, starts to rise, and she requires less and less of an incentive to remain. Finally, once the point is reached at which Gamma does not require an incentive in either a two-member or a three-member group, this decline in Beta's share of reproduction ceases. In fact, there is a very slight rise in the share of reproduction that Beta receives as Gamma's contribution increases above this point. This reflects that fact that such an increase has a slightly bigger impact in a two-member than in a three-member group, leading to an increase in the productivity of the former relative to the latter (which means that Beta has more to gain by leaving and, thus, requires more of an incentive to stay).

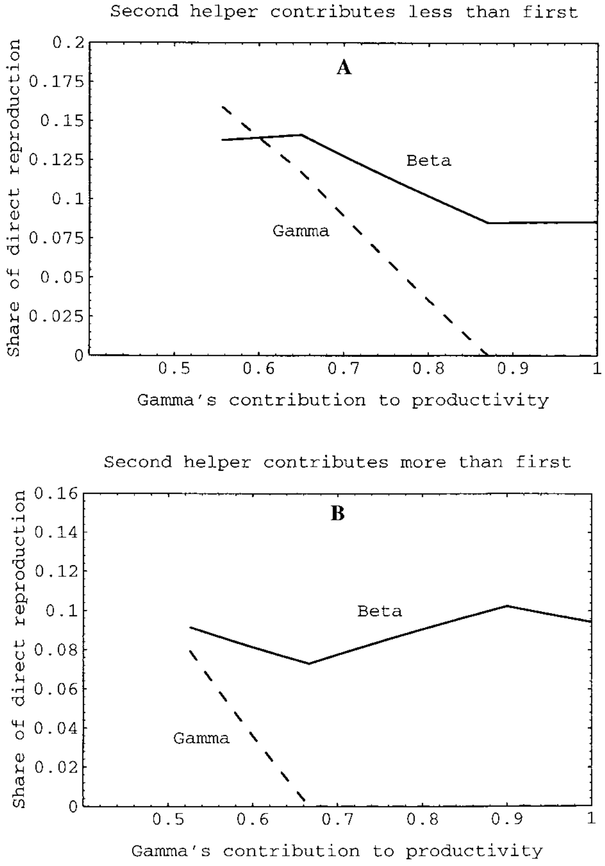

Figure 10: The proportion of total group productivity given as an incentive to Beta (*solid line*) and to Gamma (*dashed line*) when $r_{\alpha\beta} = r_{\alpha\gamma} = 0.5$ and $r_{\beta\gamma} = 0.25$, as a function of Gamma's contribution to group productivity ($k_\gamma - 1$), assuming that Beta's contribution is fixed at 0.5 (i.e., $k_\beta = 1.5$). Graph *A*, $k_2 = 1 + 0.9[(k_\gamma - 1) + (k_\beta - 1)]$, which implies that each helper makes less of a contribution in a three-member than in a two-member group. Graph *B*, By contrast, $k_2 = 1 + 1.1[(k_\gamma - 1) + (k_\beta - 1)]$, which implies that each helper makes more of a contribution in a three-member than in a two-member group. In the former case, $x_\beta = x_\gamma = 0.25$, while in the latter, $x_\beta = x_\gamma = 0.325$.

The above effects are all reversed when each helper makes proportionately more of a contribution in a three-member than in a two-member group (graph *B*). Initially, as Gamma's contribution rises, the share of reproduction she receives falls more rapidly in a three-member than in a two-member group. This increases the inclusive fitness that Beta stands to gain by remaining (relative to that which she gains by leaving), and leads to a reduction in the staying incentive that she requires. After Gamma's proportion of reproduction in a three-member group drops to zero, the share she receives in a two-member group continues to fall. This makes leaving a better option for Beta, who consequently requires greater and greater incentives to remain. Finally, once Gamma's share of reproduction reaches zero in either a two-member or a three-member group, Beta's share starts to drop once again, reflecting an increase in the relative productivity of a three-member association with Gamma's contribution (which has more impact when there are two helpers).

Discussion

The above analysis reveals that the "incentive-based" approach adopted by Vehrencamp (1983*a*, 1983*b*) and by Reeve and Ratnieks (1993; see also Reeve and Keller 1995, 1996; Reeve 1998) can readily be extended to determine the evolutionarily stable division of reproduction in a multimember group in which there is variation among subordinates. The results, however, are considerably more complex than is the case for a two-member group or for one in which all subordinates are identical. As in previous models, a subordinate is predicted to require a larger staying incentive when it is more distantly related to the dominant, has a greater opportunity to breed independently, and contributes less to group productivity. However, the share of reproduction that each individual subordinate receives depends not only on its own relatedness to the dominant, opportunity for independent breeding, and contribution to group productivity but also on the corresponding traits of the other subordinate and on the relatedness between the two. The model thus yields a number of new predictions that differ from those of previous models or have not been anticipated by them.

The Relationship between Group Size and Group Productivity

The nature of these new predictions is critically dependent on the shape of the curve relating group productivity to group size. What matters is whether the presence of a second helper contributes more or less to the productivity of the group than that of the first, that is, whether group productivity is an accelerating (concave up) or decelerating (convex up) function of group size (we assume that a three-member group is more productive than a two-member group since the dominant would otherwise have no reason to retain a second helper). This is important because it influences the relative size of the staying incentives offered to subordinates in two-member and in three-member groups (which, in turn, determines the influence of other parameters on the outcome of the model). When a second helper contributes more than the first to productivity, subordinates in a three-member group will (assuming they are related to the dominant) require less of an incentive to remain than would a lone helper since they gain more in the way of indirect fitness by helping the dominant. By contrast, when a second helper contributes less than the first, greater staying incentives are required in a three member group.

Both types of relationship have been reported in the literature. In the pied kingfisher (*Ceryle rudis*), for instance, the presence of a single helper leads to a marked increase in the reproductive success of a breeding pair, while the presence of a second subordinate contributes little extra (Reyer 1990). By contrast, in the stripe-backed wren (*Campylorhynchus nuchalis*), pairs with a single helper have very low reproductive success (little better than that of unassisted pairs), while groups with two helpers do much better (Rabenold 1990). Similar contrasts may also be found among cooperatively breeding mammals. In the golden jackal (*Canis aureus*), for example, pairs with one helper do significantly better than pairs with none, but a second helper does little to improve group productivity further (Macdonald and Moehlmann 1982). In the dwarf mongoose (*Helogale parvula*), by contrast, breeding pairs require two or more helpers (of either sex) to start reproducing effectively; one is not enough (Creel and Creel 1991). Studies of reproductive partitioning in multimember groups must therefore ascertain the shape of the group size/group productivity curve if they are to test the predictions of incentive-based models of reproductive skew.

Novel Predictions about Relatedness and Group Stability

The first new prediction to which we draw the reader's attention is that, in a multimember association, overall group relatedness may influence group stability as well as the ESS level of reproductive skew. In previous analyses of staying incentives, the stability condition for a two-member association was found to be independent of relatedness (e.g., Reeve and Ratnieks 1993). By contrast, the present model predicts that (for intermediate levels of ecological constraint and subordinate contribution to group productivity) a three-member group may prove stable only for extreme levels of overall relatedness, either low or high. This result holds whenever a second helper makes less of a contribution to group productivity than the first. The reason is that as relatedness increases, the cost to the dominant of retaining helpers drops, but it does so more rapidly for a first helper than for the second. Consequently, a three-member association becomes relatively less profitable for the dominant as relatedness increases, at least up to the level where no incentives are required in a two-member group. Beyond this point, since the incentives that must be offered to a pair of helpers continue to drop, a three-member association starts to become more profitable again.

We should thus expect to find that stable associations comprising more than two individuals tend to be composed either of distant or of much closer kin, rather than individuals of intermediate relatedness. Unfortunately, there is very little data available against which to test this prediction. Figure 11 shows a frequency histogram of estimates of mean cofoundress relatedness from nine studies of *Polistes* wasps. These estimates were obtained from published sources (Strassmann et al. 1989; Queller et al. 1990; Field et al. 1998) and cover seven species that commonly form multifoundress associations (in most cases, cofoundress relatedness was not measured directly but was estimated using the relatedness among autumn gyne nest mates; since the vast majority of spring cofoundresses are natal nest mates from the previous autumn, these values are assumed to be equal). The graph reveals some suggestion of a bimodal distribution of relatedness values, matching our prediction that multimember associations should prove stable only for low or high levels of relatedness. However, these data provide only weak support for the model because we predict a bimodal distribution of relatedness values only in associations with three or more foundresses, but we have been unable to restrict the data to groups of this kind.

The model further predicts that group stability does not depend solely on the overall or mean degree of relatedness among group members. It may be necessary to distinguish relatedness among subordinates from their mean relatedness to the dominant. For example, when a second helper contributes less to group productivity than the first, a decrease in the relatedness among subordinates (while the relatedness of each to the dominant is held constant) renders a three-member group less stable, even though a decrease in overall relatedness among group members would promote stability. The reason is that the departure of either subordinate would lead to a decrease in the share of reproduction that the other receives (for reasons discussed above). The less closely related the two helpers are, the more beneficial (or less disadvantageous) the impact of this transfer is on the fitness consequences of leaving. Consequently, the lower the degree of intersubordinate relatedness, the larger the staying incentives that the dominant must offer, and the less likely it is to do so. We would predict, for instance, that a dominant mother is less likely to retain a number of daughters as helpers if they are half-sibs than if they share the same father.

The above result suggests that, in a cooperatively breeding group comprising individuals of both sexes, skew among females may be influenced by the skew among males. If one male is able to monopolize reproduction and claim full paternity of any offspring produced by the group, then the daughters raised by a breeding female will all be full sibs. Consequently, under the conditions discussed above, they will require relatively low staying incentives to remain in the group as helpers. By contrast, if several males can claim a share of paternity, then mean relatedness among the offspring raised by the group will be lower, and they will require larger incentives to remain. In other words, high skew among males leads to high skew among females, while low skew among males leads to low skew among females. In the extreme, large groups with many subordinate females may prove stable only in situations where a single male can monopolize paternity. Intriguingly, this effect could provide a female breeder with an incentive to avoid mating with subordinate males, in order to be assured of rearing a brood of full sibs who will be easy to retain as helpers.

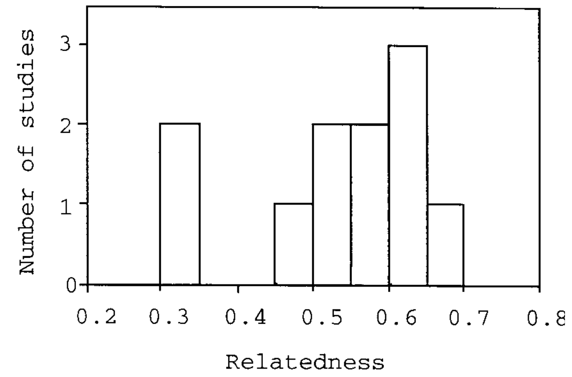

Figure 11: Frequency histogram of estimates of mean cofoundress relatedness in *Polistes* species that commonly form multimember associations. Data are taken from Queller et al. 1990 (*P. annularis*, 0.47), Field et al. 1998 (*P. bellicosus*, 0.67), and Strassmann et al. 1989 (*P. annularis*, 0.31; *P. bellicosus*, 0.34; *P. carolina*, 0.63; *P. dominulus*, 0.65; *P. dorsalis*, 0.61; *P. exclamans*, 0.56; *P. instabilis*, 0.53; we have omitted those species whose predominant mode of colony foundation is recorded as haplometrosis).

Predictions about the Partitioning of Reproduction among Subordinates

Turning to the division of reproduction among subordinates, it is clear that dyadic relationships between the dominant and individual subordinates in a group cannot be treated independently. We have already mentioned the fact that the share of reproduction a subordinate receives is influenced not only by its own relatedness to the dominant but also by its relatedness to the other subordinate (a factor that may, as discussed above, affect group stability). In addition, the other subordinate's relatedness to the dominant also affects the focal subordinate's incentive size. When a second helper contributes less to group productivity than the first, the share of reproduction that a given helper requires as a staying incentive is predicted to increase with the degree of relatedness between the dominant and other subordinates. The reverse is true when a second helper contributes more than the first (i.e., when group productivity is an accelerating function of group size). This, and the aforementioned effects of relatedness, are summarized in figure 12.

In addition to the above, the staying incentive that a subordinate requires may also be influenced by the opportunity that other subordinates have to breed independently and by their contribution to group productivity. This will occur only when relatedness in the group is not homogeneous, and the nature of the influence then depends not only on the shape of the relationship between group size and group productivity but also on the precise pattern of relatedness in the association. For instance, one subordinate's share of reproduction is likely to increase with another's opportunity for independent reproduction, provided that either the focal subordinate is more closely related to the dominant than it is to other subordinate, and a second helper contributes less to group productivity than the first, or the focal subordinate is less closely related to the dominant than it is to other subordinate, and a second helper contributes more to group productivity than the first. The probable effects of other subordinates' opportunities for independent breeding are summarized in figure 13 (note that these effects occur over only a part of the full parameter range of the model).

Turning to the influence of other subordinates' contributions to group productivity, it is very difficult to make any clearly testable predictions. The direction of the effect varies according to whether a two-member group would, under the given conditions, be stable without incentives, stable only with incentives, or unstable. Consequently, we will not attempt to summarize the model's predictions in this regard (details are given in "Results").

Reproductive Skew in Large Groups

Our analysis has focused on an association comprising a dominant and two subordinates since this is the smallest group size for which we can examine the partitioning of reproduction among subordinates who may vary in their relatedness to the dominant, their opportunity for independent breeding, and their contribution to group productivity. The same approach could readily be extended to determine the pattern of reproduction in larger groups. However, the number of parameters that can potentially influence the outcome of the model increases rapidly with group size: in an association with n subordinates, we must specify $n\ (n+1)/2$ coefficients of relatedness (or more, if we allow for asymmetries in relatedness between pairs of group members), in addition to terms $x_1, \ldots, x_n$, which specify the opportunity that each subordinate has for independent breeding, and a series of k terms that give the productivity of the dominant in association with each possible combination of subordinates (ranging from zero to n in number). A full analysis of all possible outcomes is thus unfeasible for larger groups.

The main results of the present analysis, however, can be generalized to the case of cooperatively breeding groups that contain more than three members. When considering an association with n subordinates, the relative contributions made by the $(n-1)$th and nth helpers (i.e., the shape of the group size/productivity curve at that point)

	Focal subordinate's relatedness to dominant	**Focal subordinate's relatedness to other subordinates**	**Other subordinates' relatedness to dominant**
Presence of a second helper contributes *less* than first to group productivity	↓	↓	↑
Presence of a second helper contributes *more* than first to group productivity	↓	↑	↓

Figure 12: Effects of the coefficients of relatedness among group members on the size of staying incentive required by individual subordinates (depending on whether a second helper contributes more or less than the first to group productivity). A downward-pointing arrow indicates that an increase in the coefficient in question leads to a decrease in incentive size; an upward-pointing arrow, that it leads to an increase in incentive size (note that these effects apply only when all subordinates are to some degree related to the dominant).

	Focal subordinate *more* closely related to dominant than to other subordinate	**Focal subordinate *less* closely related to dominant than to other subordinate**
Presence of a second helper contributes *less* than first to group productivity	↑	↓
Presence of a second helper contributes *more* than first to group productivity	↓	↑

Figure 13: Effects of other subordinates' opportunities for independent breeding on the share of direct reproduction that the focal subordinate receives, depending on the shape of the relationship between group size and group productivity and on whether the focal subordinate is more or less closely related to the dominant than to the other subordinates. An upward-pointing arrow indicates that the focal subordinate's incentive size increases with other subordinates' opportunities for independent breeding; a downward-pointing arrow, that it decreases.

will determine whether the departure of any one subordinate would lead to an increase or a decrease in the reproductive shares obtained by the others. Just as in the present analysis, this will determine whether increasing relatedness among subordinates leads to an increase or a decrease in the staying incentives that they require: a decelerating relationship between group size and productivity will result in a positive relationship between skew and intersubordinate relatedness. Similarly, the shape of the group size/productivity curve will also determine whether a focal subordinate's share of reproduction increases or decreases with the relatedness of other subordinates to the dominant and with the opportunities that other subordinates have to breed independently. In other words, while the present analysis focuses on a group with only two subordinates, this is sufficient to determine how the share of reproduction obtained by any one helper will be influenced by the traits of others, even in a much larger group.

Future Modeling Possibilities

We conclude by drawing attention to some of the present model's key assumptions that could be relaxed or modified in future analyses of reproductive partitioning. First, we have assumed a monarchical power structure within the group, in which Alpha controls the allocation of direct reproduction to both Beta and Gamma, who are equally ranked (i.e., neither can influence the allocation of direct reproduction to the other). An alternative possibility, suggested by both Vehrencamp (1983*a*) and Reeve and Ratnieks (1993), would be a "hierarchical" group, in which Alpha determines the total share of reproduction that the two subordinates obtain, but Beta (the higher-ranking subordinate) determines what proportion of this share is allocated to Gamma (the lower-ranking subordinate). Examples of both natural monarchies and hierarchies have been reported. Colonies of the naked mole rat (*Heterocephalus glaber*), for example, appear to represent the former. Breeding is restricted to the dominant female, who also performs 95% of all dominance assertion behavior. Moreover, following the removal of the breeding female from a colony, there was no clear successor, suggesting the absence of a strict dominance hierarchy among the various subordinates, a number of whom began to show ovarian activity once they were no longer exposed to the inhibitory effect of the dominant (Margulis et al. 1995). By contrast, breeding groups of the dwarf mongoose (*Helogale parvula*) may represent natural hierarchies. While dominant males defend dominant oestrous females and thereby claim a high proportion of group reproduction, subordinate males also fight among themselves over opportunities to mate with subordinate females and exhibit a definite dominance hierarchy, with higher-ranking individuals winning almost all encounters (Creel et al. 1992). It would therefore be very interesting to compare the levels of skew predicted in these different power structures.

Second, more complex possibilities also arise if one allows for incomplete control by higher-ranking individuals of the reproductive opportunities open to lower-ranking group members. Cant (1998) and Reeve et al. (1998) have developed models of skew in a two-member group in which the dominant has incomplete control over subordinate reproduction (a situation that may be common, particularly among vertebrates; see Clutton-Brock 1998).

It would be useful to extend this kind of approach to deal with larger associations, allowing consideration of the partitioning of reproduction among subordinates who may vary in their degree of power or control.

Third, we have focused on a three-member group whose membership is fixed, subject only to the possibility of departure on the part of Beta and Gamma. It would, however, be of great interest to allow for sequential (and uncertain) addition of helpers to a group that initially comprised perhaps a single breeder, by either arrival of adults or recruitment of juveniles. Ultimately, by incorporating the possibility of Alpha's dying and allowing one of the subordinates in the group to accede to dominant status in that event (perhaps with some possibility of usurpation by an intruding individual), one could embed the model in a dynamic framework; this would yield predictions about the change in skew over time as a group develops (see, e.g., Lucas et al. 1997 for an application of dynamic optimization in the context of cooperative breeding among mammals).

Finally, we have assumed that subordinates can freely choose to join or leave the group. This ignores the fact that it may sometimes be possible for one group member to forcibly eject another or to prevent a new arrival from joining the association. Given our assumption that subordinates can only acquire a share of reproduction if the dominant yields it to them, it is unlikely that Alpha will ever have to forcibly exclude or eject a helper (withholding reproduction is likely to be enough to encourage departure). Moreover, since subordinates are assumed to boost group productivity, Alpha has little to gain by doing so. One subordinate, however, may well stand to gain by excluding or ejecting another. "Insider-outsider" conflicts among subordinates are thus possible (see Higashi and Yamamura 1993), and it would be of great interest to incorporate them in the model.

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