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Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders?

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Optimal skew models explain reproductive sharing within social groups as resulting from reproductive incentives given by controlling dominants to subordinates in return for peaceful cooperation. We explore two versions of an alternative, the incomplete control model, for the evolution of reproductive sharing within groups. In this model, dominants have only limited control over the allocation of reproduction and must expend effort to increase their share of the total group output. We show that, when the relatedness between dominant and subordinate is symmetrical, (1) the subordinate's fraction of reproduction either increases with, or is insensitive to, the subordinate's genetic relatedness, r, to the dominant in both versions of the incomplete control model, whereas the subordinate's fraction of reproduction decreases with increasing r in the optimal skew model, (2) the subordinate's share of reproduction in the incomplete control model must exceed that in the optimal skew model, and (3) ecological factors affecting solitary breeding success do not directly affect the subordinate's share of reproduction in incomplete control model but do in the optimal skew model. When dominant–subordinate relatedness is asymmetrical (as is often the case in parent–offspring associations), the incomplete control model predicts no reproduction by the subordinate offspring regardless of group size for groups containing any mixture of unrelated and full-sibling subordinates, whereas the optimal skew models predict that such reproduction is possible when the group size is three or more. The available evidence indicates a negative relationship between relatedness and a subordinate's reproductive share in both vertebrate and hymenopteran societies, apparently supporting the predictions of the optimal skew, not incomplete control, class of models. However, such a negative relationship is not necessarily inconsistent with the incomplete control model when, as is true for some vertebrate studies, it results from a comparison of skews in genetically monogamous, nonincestuous groups of parents and their offspring (asymmetric relatednesses) with skews in groups of nonkin (symmetric relatednesses). Both models predict higher skews in parent–offspring associations. Occasional reproduction by subordinate offspring in groups of asymmetrical relatedness when such groups are larger than dyads is more consistent with the optimal skew model, however. Overall, current data on reproductive skew and its relationships to intragroup aggression and ecological constraints support the optimal skew model, but more data are needed to rule out the incomplete control model. These models are examples of two different general views of intrasocietal evolution: the tug-of-war view, in which group members engage in a struggle over resources, and the transactional view, in which group members exchange parcels of reproduction to induce beneficial behavior from each other. *Key words:* conflict, cooperation, cooperative breeding, eusociality, optimal skew, reproductive concessions, reproductive skew, sociality. *[Behav Ecol 9:267–278 (1998)]*

Much recent interest has focused on the factors that influence the evolution of reproductive partitioning among group members, in particular the degree to which shared reproduction is biased in favor of dominant breeders (Bourke and Franks, 1995; Bourke and Heinze, 1994; Bourke et al., 1997; Creel and Waser, 1991; Emlen, 1982b, 1984, 1995, 1996, 1997b; Emlen and Vehrencamp, 1983; Heinze, 1995; Heinze et al., 1995; Jamieson, 1997; Keane et al., 1994; Keller and Reeve, 1994; Reeve, 1991, 1998; Reeve and Keller, 1995, 1996; Reeve and Nonacs, 1992; Reeve and Ratnieks, 1993; Vehrencamp, 1983a,b). In high-skew societies, direct reproduction is concentrated in one or a few dominant breeders in the group; in low-skew societies, reproduction is distributed more evenly among group members. Models of "optimal skew" in reproduction attempt to explain the degree of skew by predicting the conditions under which dominant breeders should yield just enough reproduction to a subordinate to make it favorable for the subordinate to stay in the group and cooperate peacefully rather than to leave the group and reproduce independently or fight for exclusive control of the group's resources. Reproductive payments that prevent subordinates from leaving are called staying incentives; payments that prevent subordinates from fighting to the death for complete control of colony resources are called peace incentives (Reeve and Ratnieks, 1993).

The first models of the evolution of reproductive skew analyzed how ecological constraints on solitary reproduction, genetic relatedness of potential breeders, and productivity advantages of peaceful association should influence the magnitudes of staying incentives in vertebrate and invertebrate societies (Emlen, 1982b, 1984; Emlen and Vehrencamp, 1983; Reeve, 1991; Vehrencamp, 1979, 1983a,b). Reeve and Ratnieks (1993) extended these models by examining how relative fighting ability among group members will interact with the above factors to influence the reproductive skew via peace incentives. The general conclusions of these classical skew models are that the skew should increase (i.e., the reproduction should become less equitable) as (1) the relatedness between dominants and subordinates increases, (2) the proba-

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bility of successful solitary reproduction by the subordinate decreases (i.e., for stronger ecological constraints), (3) the subordinate's contribution to colony productivity increases (because the larger this contribution, the less the subordinate has to be compensated), and (4) the subordinate's relative fighting ability decreases. Reeve and Keller (1995) recently showed that the asymmetry in relatedness occurring in mother–daughter associations versus sibling associations should tend to increase the degree of skew in the former. Emlen (1996) pointed out that inbreeding avoidance will reinforce the high skew in parent–offspring associations by shutting down intragroup mating options; Reeve and Keller (1996) showed that high skew is predicted even when subordinates can mate outside of the group and then rear outbred offspring within the group. Recent tests of these predictions have generated striking, but preliminary, support for classical optimal skew theory (Bourke and Heinze, 1994; Bourke and Franks, 1995; Bourke et al., 1997; Creel and Waser, 1991; Emlen, 1995, 1996, 1997b; Jamieson, 1997; Keane et al., 1994; Keller and Reeve, 1994; Reeve, 1998; Reeve and Keller, 1995; Reeve and Nonacs, 1992).

Finally, the classical optimal skew theory has recently been expanded to encompass the case in which dominants in two or more colonies compete for the services of a helping subordinate (the "bidding game"; Reeve, 1998). In such a case, breeder–subordinate relatedness is not predicted to affect the reproductive skew, and, in further contrast to predictions of the original skew models, the skew is predicted to decrease as the subordinate's contribution to colony productivity increases.

Both the classical optimal skew model and the bidding game model explain reproductive sharing as the offering of reproductive incentives by dominants to subordinates, and thus these models implicitly assume that dominants are in control of the distribution of reproduction. Such models can also be called "reproductive concessions" models (Clutton-Brock T, in press) because the dominant concedes reproduction to the subordinate in return for the latter's cooperation. Below we explore an alternative model for the evolution of reproductive sharing within groups in which dominants have only limited control over the allocation of reproduction within groups, and reproductive sharing simply reflects a dominant's inability to monopolize the group's reproduction. We show that this "incomplete control" model makes some predictions different from those of the existing skew models. We then assess which of the two models is best supported by existing data on reproductive sharing in both vertebrate and invertebrate social groups. Finally, we point out that the two different models of reproductive skew are examples of two different general classes of models of intra-colony conflict: tug-of-war versus transactional models.

Role of genetic relatedness

As in the optimal skew models, we begin with the assumption that two group members differ in dominance (i.e., in some characteristic, such as resource-holding power, that potentially leads to an asymmetry in reproduction). In optimal skew models, the amount of reproduction yielded by a dominant to a subordinate is predicted to depend upon (1) the relatedness between dominant and subordinate, (2) the subordinate's prospects for successful reproduction if it leaves the group (i.e., the severity of ecological constraints), and (3) the productivity advantages of peaceful association. Thus, three parameters enter into the basic skew model for dyadic groups: r is the (symmetrical) relatedness of the dominant to the subordinate; x is the expected solitary reproduction by a potential subordinate (relative to a standardized reproductive output equal to 1 for a dominant that is not joined by the subordinate), with lower values of x indicating harsher ecological constraints on independent breeding (we assume that $x \leq 1$), and k is the overall direct reproduction of a dyad (again relative to a standardized reproductive output equal to 1 for a lone dominant). The resulting personal reproductive outputs for both parties are summarized in Table 1.

Table 1
Reproductive outputs for dominant and subordinate in the classical optimal skew model

	Subordinate stays	Subordinate leaves
Dominant	$k(1 - p_s)$	1
Subordinate	kp_s	x

Also as for optimal skew models, we will employ Hamilton's rule for deciding which of two alternative strategies will be favored by selection. That is, strategy i will be favored over strategy j if

$$(P_i - P_j) + r(K_i - K_j) > 0, \quad (1)$$

which is equivalent to

$$P_i + rK_i > P_j + rK_j, \quad (2)$$

where r is the coefficient of relatedness between the two interactants, P_i (or P_j) is the personal reproduction associated with strategy i (or j), and K_i (or K_j) is the other party's reproduction if strategy i (or j) is performed. Parker (1989) has shown in an important theoretical analysis that use of the above additive version of Hamilton's rule is correct if dominants and subordinates can be viewed as being in different roles, with role being assigned randomly with respect to genotype, and if gene expression is strictly conditional upon role.

In the classical skew model, the proportion, p_s, of overall direct reproduction yielded to the subordinate in a stable association is that which gives the subordinate just sufficient incentive to remain in the association rather than leave and attempt to reproduce independently. This is the "staying incentive" of Reeve and Ratnieks (1998) (previously called the fitness "forfeited" by Emlen, 1982b). (For simplicity, we do not consider here the case of peace incentives offered by dominants to subordinates to prevent a fight to the death for exclusive control of the group's resources; see Reeve and Ratnieks, 1998.) If ecological constraints are strong, corresponding to the condition $x < r(k - 1)$, the subordinate will stay in the association with no reproduction, that is, $p_s = 0$ (maximum skew). (The inequality is obtained by solving Hamilton's rule for the subordinate, using the offspring numbers in Table 1 with $p_s = 0$.) If ecological constraints are moderate, i.e., $r(k - 1) < x < k - 1$, then the subordinate will receive a staying incentive, the magnitude of which is

$$p_s = [x - r(k - 1)]/k(1 - r), \quad (3)$$

which is obtained by using Hamilton's rule and Table 1 to solve for the minimum fraction of reproduction required to make staying (versus solitary breeding) favorable for the subordinate. The staying incentive decreases in magnitude (meaning that the skew increases) as the relatedness, r, increases, the total group output, k, increases, and the solitary output, x, decreases. If ecological constraints are weak, corresponding to the condition $x > k - 1$ (requiring $k \leq 2$), the subordinate is favored to leave and reproduce solitarily (Emlen, 1982a; Reeve and Ratnieks, 1998; Vehrencamp, 1983a).

Now consider a model in which the dominant has incom-

plete control over the subordinate's reproduction. Suppose that $x < k - 1$ but that the dominant cannot profitably reduce the subordinate's reproduction to the "break-even point," p_e, at which staying is just favored over solitary reproduction, with the result that the subordinate's fraction of reproduction always exceeds its staying incentive. (If the dominant could profitably push the subordinate's reproduction to this lower limit, the classical optimal skew model would apply because the dominant must always yield the staying incentive, lest it lose the subordinate and thus any reproductive benefits conferred by the latter.) The dominant must decide how much effort to expend in increasing its fraction of the total reproduction at the expense of total group output [see Reeve and Nonacs (1997) for a model of how such selfish effort should vary with the value of the subordinate to the dominant]. The subordinate likewise must decide how much effort to expend in increasing its share of the reproduction (also at the expense of total group output). Increasing effort by either the dominant or subordinate is likely to reduce total group output by increasing the fraction of the dyad's total energy reserves that is channeled into selfish augmentation of the share of reproduction (e.g., via physical conflict over access to group resources) instead of into offspring production and parental and alloparental care. This loss of total output may place a limit on the optimal effort for the dominant (and perhaps on that of the subordinate as well), and sharing of reproduction may result.

To consider the latter possibility formally, we constructed two explicit models in which the dominant and subordinate use part of the group's resources to engage in a "tug-of-war" over the share of reproduction within the group. We assumed for simplicity that the group's total productivity is a linearly increasing function of the fraction of the group's resources that is not expended in the tug-of-war. In the first model, the subordinate inefficiency model, we assume that subordinates are less efficient than dominants in converting resources to an increased share of reproduction. In the second model, the restricted access model, we assume equal efficiencies, but that the subordinate controls at most a fixed fraction f, and the dominant a greater fraction $1 - f$, of the resources.

Subordinate inefficiency model

In this model, dominance is determined by resource-holding power. The dominant freely allocates a fraction x, and the subordinate freely allocates a fraction y, of the group's resources to the tug-of-war (x and y are thus the selfish efforts described above). The fraction of reproduction going to the dominant is $x/(x + by)$ and to the subordinate is $by/(x + by)$; i.e., the net skew depends on the ratio of resources allocated by the two interactants to the tug of war (we stipulate that if both x and y equal zero, reproduction is shared equally). The constant b is a number greater than zero and less than or equal to one, reflecting the subordinate's possibly greater inefficiency in converting resources to an increased share of the reproduction (e.g., its smaller relative fighting ability). Thus, the greater the dominant's efficiency (e.g., relative fighting ability), the smaller b is, and the greater is the dominant's share of the reproduction (i.e., its net "pull" in the tug-of-war) for a given x and y. Note that, by contrast, the dominant's efficiency has no effect on the staying incentive of the classical optimal skew model.

The discrete form of Hamilton's rule indicates that, for a member of a dyadic group, selection should maximize the inclusive fitness $pk + r(1 - p)k$ or, equivalently, $k[r + (1 - r)p]$ where p is the selfish share of reproduction and k is the total group output. By the assumptions of the subordinate inefficency model, the dominant's inclusive fitness is thus

$$I_d = (1 - x - y)\,[r + (1 - r)x/(x + by)] \qquad (4)$$

and the subordinate's inclusive fitness is

$$I_s = (1 - x - y)\,[r + (1 - r)by/(x + by)] \qquad (5)$$

We seek the Nash equilibrium (x^*, y^*) (i.e., the values x^* and y^* that are mutual best replies; Mesterton-Gibbons, 1992), with the payoffs being calculated from Equations 4 and 5. In this case, the Nash equilibrium is obtained by finding the positive values x^* and y^* satisfying

$$\partial I_d/\partial x = 0; \qquad \partial I_s/\partial y = 0 \quad \text{at } x = x^*; \quad \text{and} \quad y = y^*.$$

These solutions are

$$x^* = \frac{b}{2(1 - b)}\left[\frac{2 - r(1 - b)}{\sqrt{r^2(1 - b)^2 + 4b}} - 1\right]$$

and

$$y^* = \frac{1}{2(1 - b)}\left[1 - \frac{2b + r(1 - b)}{\sqrt{r^2(1 - b)^2 + 4b}}\right] \qquad (6)$$

The evolutionarily stable skew (dominant's share of reproduction) is

$$x^*/(x^* + by^*) = \frac{2}{2 - r(1 - b) + \sqrt{r^2(1 - b)^2 + 4b}} \qquad (7)$$

A rather counterintuitive prediction of the model (seen from a plot of $y^* - x^*$ for the biologically meaningful ranges of r and b) is that subordinate effort should always be higher than the dominant's effort ($y^* > x^*$), despite the fact that the subordinate's inefficiency causes it to always capture less than half of the total reproduction ($by^* < x^*$). Thus, the model predicts higher levels of attempted selfishness by subordinate than by dominant individuals.

All biologically meaningful solutions ($0 \le r < 1$ and $0 \le b < 1$) for the dominant effort and the skew are shown as the surfaces in Figure 1. Figure 1 shows that the dominant's effort decreases with increasing r and increases with the subordinate efficiency factor, b (the latter occurs because a subordinate with a higher b is more competitive, requiring greater selfishness by the dominant to secure a given fraction of the reproduction). It is also shown that the evolutionarily stable skew declines with increasing b, but is virtually insensitive to relatedness. The maximum effect of relatedness is observed when $b = 0.12$ (i.e., for exceptionally weak subordinates), but even for this value of b, the dominant's share of reproduction only increases by 0.15 as relatedness increases from 0 to 1. The principal conclusion of this tug-of-war model is that relatedness will have virtually no effect on reproductive skew, primarily because relatedness changes the evolutionarily stable dominant and subordinate efforts (x^*, y^*) in the same direction and to extents that are roughly inversely proportional to their effects on skew (see appendix).

Our conclusions appear robust with respect to variation in the assumptions of the subordinate inefficiency model. For example, we assumed that the share of reproduction depended on the ratio of energies invested in the tug-of-war. It is possible that in some contexts the relevant ratio is some power function of the invested energies with the power being other than 1. However, this makes little difference to the prediction that skew will be essentially insensitive to relatedness (Figure 2). In addition, we might assume that only some fraction of the colony resources are economically contestable and that the tug-of-war applies only to the remaining fraction; such an assumption would only further dilute the extremely weak relationship between skew and relatedness. This insensitivity to relatedness contrasts sharply with the reproductive skew predicted by the optimal skew models (Figure 3).

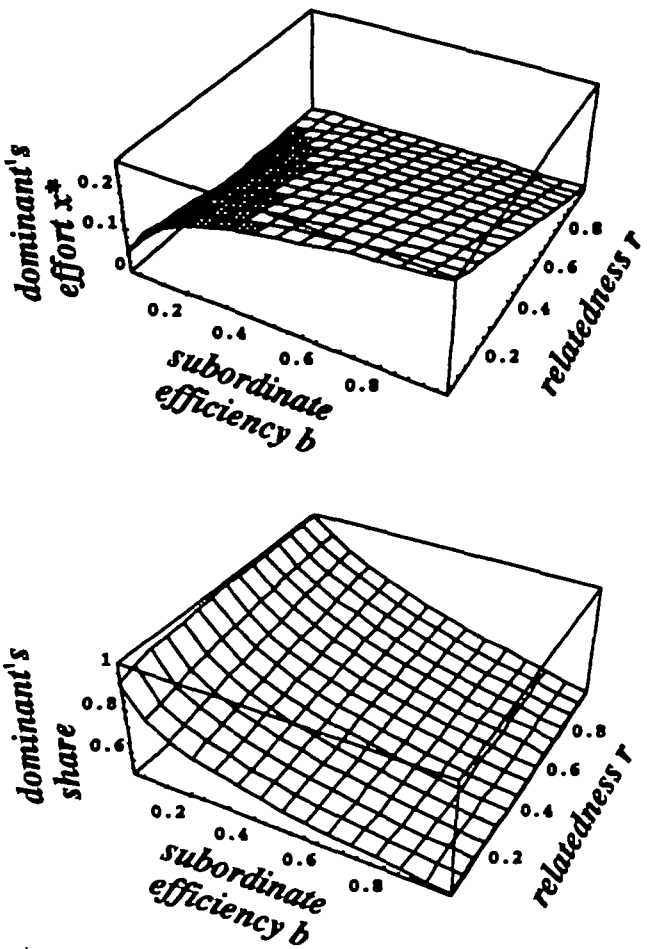

Figure 1
Subordinate inefficiency tug-of-war model (symmetrical relatedness between dominant and subordinate). (Top) Dominant's evolutionarily stable effort as a function of both subordinate's fighting efficiency, b, and their genetic relatedness, r; (bottom) Evolutionarily stable fraction of dyad reproduction going to the dominant as a function of both subordinate's fighting efficiency and their genetic relatedness.

Arbitrary group size and asymmetrical relatedness. The preceding model was developed for the special case of symmetrical relatedness and dyadic groups. The model can be generalized for groups of any genetic composition and arbitrary size n by finding the combination of n x values that are Nash equilibria (obtained as above) corresponding to the n inclusive fitness expressions, with the inclusive fitness of the jth individual given by

$$I_j = \left(1 - \sum_{i=1}^{n} x_i\right)\left[\frac{\sum_{i=1}^{n} r_i b_i x_i}{\sum_{i=1}^{n} b_i x_i}\right], \qquad (8)$$

where r_i is the relatedness of the focal individual to the ith individual's offspring, divided by the focal individual's relatedness to its own offspring (henceforth referred to as the "effective relatedness"), b_i is the ith individual's efficiency, and x_i is the ith individual's effort. Numerical results from the more general model suggest that the insensitivity of skew to relatedness is not restricted to groups of two members but will usually occur unless group sizes are relatively large and subordinates are very inefficient (Figure 4).

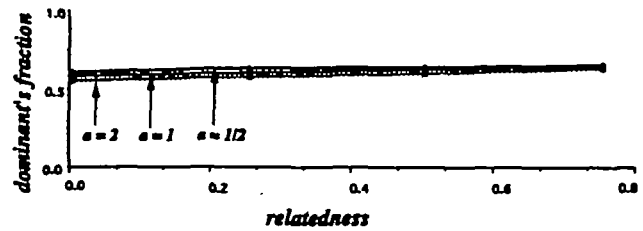

Figure 2
Insensitivity of dominant's fraction of reproduction ($x^{*a}/[x^{*a} + by^{*a}]$) to the value of the exponent a in the subordinate inefficiency tug-of-war model. $b = 0.50$ (symmetrical relatedness).

The general model can be used to analyze the case of asymmetrical relatedness between dominant and subordinate. Asymmetrical relatedness refers to associations where the participants are unequally related to each other's offspring, as when the dominant is a parent of the subordinate. The definition of r_i allows for asymmetrical relatedness: assuming single mating and no inbreeding, an offspring is effectively related to its parent by 1.0, because young full siblings are ge-

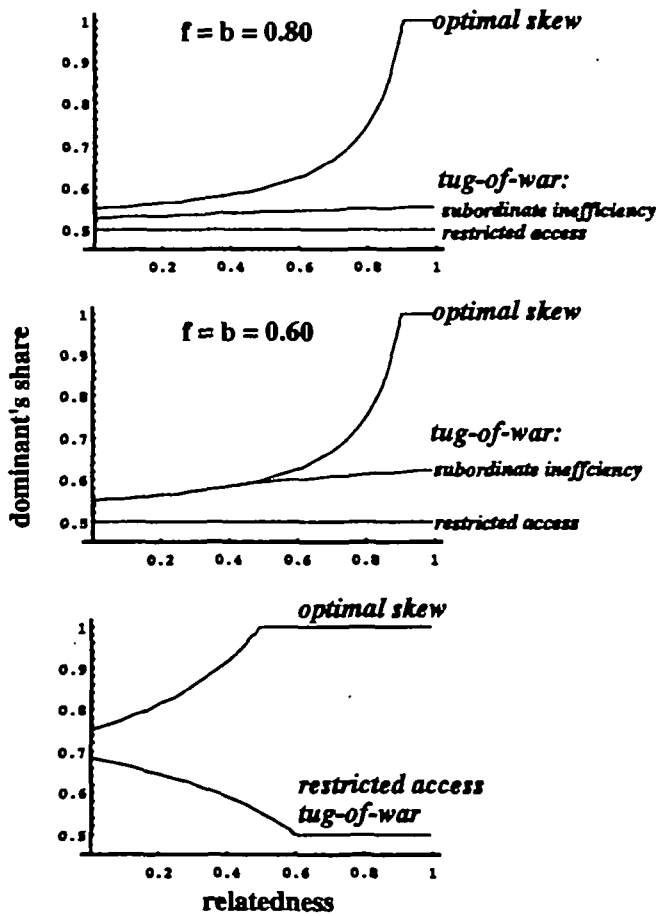

Figure 3
Dominant's share of reproduction versus genetic relatedness in the optimal skew model compared to the subordinate inefficiency and restricted access tug-of-war models (symmetrical relatedness). (Top and middle) $x = 0.50$; $k = 2$. (Bottom) Opposing effects of relatedness in the optimal skew and some solutions to the restricted access models: $x = 0.50$; $k = 2$; $f = 0.10$. Note that the dominant's share in the tug-of-war (incomplete control) models cannot exceed that in the optimal skew model lest the dominant lose the subordinate and thus the benefits of grouping.

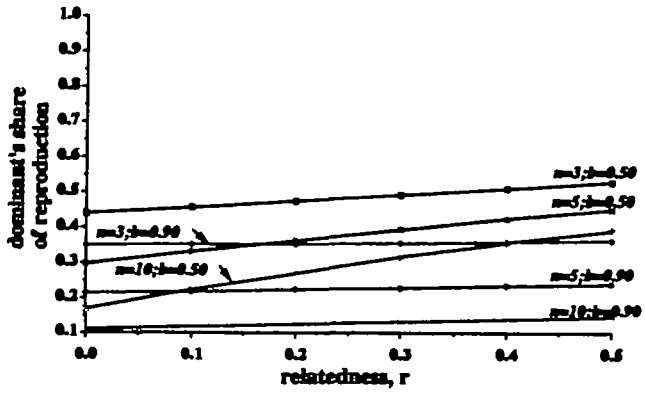

Figure 4
Insensitivity of dominant's share of reproduction to relatedness in the subordinate inefficiency model across differently sized groups (symmetrical relatedness; groups include one dominant and multiple subordinates with equal efficiencies b).

netically as valuable as offspring, whereas the parent is related to the offspring by only 0.50. Remarkably, for many frequently occurring kinds of groups (e.g., any mixture of full sibling and unrelated subordinates), and whenever the parent has higher efficiency or access to more resources than its subordinate offspring, the evolutionarily stable effort by the offspring will be zero, regardless of the size or genetic composition of the rest of the group (see appendix). This occurs because a subordinate offspring's genetic interests completely overlap with those of the parent in this situation (effective relatedness, r_e to parent = 1.0), but the interests of the parent do not completely overlap with that of the offspring ($r_i = ½$). The result is that the parental optimum (i.e., some positive effort by the parent and zero effort by the offspring) is an optimum for the offspring as well. Unfortunately, the optimal skew model also predicts zero reproduction of a subordinate offspring when the dominant parent is the only other member of the group (Reeve and Keller, 1995). Thus, complete skew is predicted for an outbreeding parent–offspring dyad by both the optimal skew and incomplete control models, so such skews cannot be used to distinguish between the two models.

However, the predictions of the two models can diverge even for parent–offspring groups under two special conditions. First, the asymmetry in relatedness within parent–offspring associations can disappear whenever (1) a mate change occurs between successive breedings [i.e., a subordinate offspring has the same effective relatedness to the parent (0.25/0.50 = 0.50) as the parent does to it (0.25/0.50 = 0.50) when the subordinate's young siblings are half-siblings], or (2) incestuous breeding occurs between the dominant parent and subordinate offspring (e.g., in diploid species, a non-inbred parent and its offspring have effectively equal relatedness to their joint offspring). In these special cases, the symmetrical-relatedness classical skew models will still apply.

Second, when groups with asymmetrical relatedness consist of more than two individuals, a subordinate offspring can receive some reproduction in the optimal skew model in cases where it cannot in the incomplete control model. To see this for one special case of the optimal skew model, suppose there is one dominant parent and m (≥ 2) full-sibling subordinate offspring. All breeders avoid inbreeding. Let p_x and k_x be the staying incentive for each subordinate and the group output, respectively, for a group of size g. Using Hamilton's rule, the staying incentive for each subordinate in a group of size m is

$$p_m = \frac{2(k_m - k_{m-1}) + (m-1)k_{m-1}p_{m-1} - 2x}{k_m(m-1)}. \quad (9)$$

This staying incentive will be positive and yielded by the dominant under the condition $a/(m+1) < x < a/2$ where $a = 2(k_m - k_{m-1}) + k_{m-1}p_{m-1}(m-1)$. Thus, reproduction by subordinate offspring in the presence of a dominant parent is possible in the optimal skew model for $m>1$ but not in the incomplete control model when subordinates are full siblings.

Restricted access model

In the restricted access model, dominance is determined by a prior asymmetry in accumulated resources. We begin with the case of symmetrical relatedness in a dyadic group and assume that the subordinate has access to only a proportion f ($< ½$) of the group's resources, of which it freely allocates a fraction, w, to the tug-of-war, and the dominant has access to a greater proportion $(1 - f)$ of the group's resources, of which it freely allocates a fraction, z, to the tug-of-war; in this model, dominant and subordinate have equivalent efficiencies. For example, this situation might arise if a dominant and subordinate form an association only after they have procured and stored resources to be used in both reproduction and parental care (with the dominant having stored more resource). For example, this situation might apply to associations of co-founding ant queens. The tug-of-war might then consist of resource-depleting competition over the apportionment of parentage in a clutch that will subsequently receive joint parental care.

By the above assumptions, the dominant's inclusive fitness is now equal to

$$I_d = [1 - (1-f)z - fw]\left[r + (1-r)\frac{(1-f)z}{(1-f)z + fw}\right], \quad (10)$$

and the subordinate's inclusive fitness is

$$I_s = [1 - (1-f)z - fw]\left[r + (1-r)\frac{fw}{(1-f)z + fw}\right]. \quad (11)$$

We then solve for the evolutionarily stable solutions z^* and w^*, as above. The solutions in this case are

$$z^* = (1-r)/4(1-f) \quad \text{and} \quad w^* = (1-r)/4f \quad \text{if } r \geq 1 - 4f,$$

and

$$z^* = \frac{\sqrt{f(1-r)} - f}{1-f} \quad \text{and} \quad w^* = 1 \quad \text{if } r < 1 - 4f. \quad (12)$$

As in the subordinate inefficiency model, the evolutionarily stable effort of the subordinate always exceeds that of the dominant, despite the fact that the subordinate controls a smaller fraction of the resources. Thus, both models predict higher levels of attempted selfishness by subordinates than by dominants.

If $r \geq 1 - 4f$, the somewhat surprising result is that the evolutionarily stable share of the dominant's reproduction—i.e., $z^*(1-f)/[z^*(1-f) + fw^*]$—is exactly ½, independently of relatedness or the subordinate's fraction of resources f. This is because as relatedness increases, both dominant and subordinate efforts decrease. A comparison of w^* and z^* in Equation 12 shows that the subordinate's effort decreases faster than the dominant's effort as relatedness increases. However, the faster decrease for a subordinate is exactly compensated by the smaller effect of the subordinate's effort on the resulting skew (i.e., by the fact that the subordinate's effort is weighted by just f compared to greater value $1 - f$ for the dominant).

If $r < 1 - 4f$, the subordinate's evolutionarily stable effort

is a constant $w^* = 1$, corresponding to an endpoint maximum, and the share of the dominant's reproduction is

$$1 - \sqrt{\frac{f}{1 - r}}, \tag{13}$$

which decreases with increasing r. Thus, as r increases in this model, the skew decreases until r exceeds the threshold $1 - 4f$, at which point the reproduction is perfectly equitable regardless of further increases in relatedness (Figure 3). Thus, increased relatedness tends to lead to lower skew. In fact, it is generally true that, when the subordinate's effort is constant, the dominant's optimal effort and thus the skew should decrease as r increases (see appendix). In summary, in the restricted access model, skew either is constant or decreases as relatedness between dominant and subordinate increases.

Arbitrary group size and asymmetrical relatedness. The restricted access model was developed for the special case of symmetrical relatedness and dyadic groups. The model can be generalized for groups of any genetic composition and arbitrary size n by finding the combination of values of x that are Nash equilibria (obtained as above) corresponding to the n inclusive fitness expressions, with the inclusive fitness of the jth individual given by

$$I_j = \left(1 - \sum_{i=1}^{n} f_i x_i\right)\left[\frac{\sum_{i=1}^{n} r_i f_i x_i}{\sum_{i=1}^{n} f_i x_i}\right]. \tag{14}$$

The general model can be used to analyze the case of asymmetrical relatedness between dominant and subordinate, just as in the subordinate inefficiency model. As in the latter model, the evolutionarily stable effort by a subordinate offspring is zero whenever it is in a group with a dominant parent and any mixture of full-sibling and unrelated subordinates (appendix). Again, this prediction is not necessarily true in the optimal skew model when groups are larger than dyads (see Equation 9).

Overall, we conclude, from both the subordinate inefficiency and the restricted access tug-of-war versions of the incomplete control model, that increasing relatedness either decreases or does not appreciably affect the reproductive skew when relatedness between dominant and subordinate is symmetrical. Both predictions contrast with the corresponding prediction of the classical optimal skew models (Figure 3). It is possible that more complicated models of incomplete control could be constructed to predict a positive effect of relatedness on skew, but we think it is telling that the simplest and most intuitive models we could construct make the prediction of either virtually no effect or a negative effect. The latter predictions are likely to have considerable generality for the following reasons: as relatedness increases in incomplete control models, either (1) the dominant and subordinate both should decrease their selfish efforts, with the result that there is little net effect on skew, or (2) only the dominant should decrease its effort (because the subordinate always exerts its maximal effort), with the result that there is a negative effect of relatedness on skew. As indicated by our analyses, it is unlikely that the dominant will exhibit a constant, maximal effort and the subordinate a flexible effort (leading to a positive relationship between relatedness and skew). The dominant, by definition, has greater fighting ability or access to resources than does the subordinate; thus, its optimal effort is less likely to be pushed to an upper limit than is the subordinate's.

The incomplete control and optimal skew models also make distinct predictions in the case of asymmetrical relatedness. When there are more than two group members, the subordinate offspring is often predicted to reproduce in the optimal skew (see Equation 9) but not in the incomplete control models (see Appendix).

Optimal skew versus incomplete control models: role of ecological constraints

The parameter x (solitary reproductive output standardized relative to the output of a lone dominant) is an inverse measure of ecological constraints on independent breeding. In the optimal skew model, x profoundly affects the reproductive skew because the dominant concedes just enough reproduction to the subordinate for the latter to reach its "break-even point," and this point obviously depends on x (see Equation 3). In the incomplete control model, by contrast, the subordinate always reproduces above the break-even point (i.e., obtains more than its staying incentive), and the partitioning of reproduction is not directly influenced by x. If the dominant reduces the subordinate's reproduction to this "break-even point," the incomplete control model becomes identical to the optimal skew model. Note that even in the incomplete control models, the dominant can never force the subordinate to obtain less than its staying incentive (Equation 3) because the subordinate would then be favored to leave the group and attempt to breed independently. This would deprive the dominant of the assumed benefits of grouping.

Optimal skew versus incomplete control models: summary of predictions

The classical optimal skew and incomplete control models make very different predictions about the regulation of the subordinate's share of reproduction, both when relatedness is symmetrical and when it is asymmetrical.

Symmetrical relatedness. According to the incomplete control model, the subordinate's fraction of reproduction will either increase with, or be quite insensitive to, the relatedness, r, whereas the subordinate's fraction of reproduction will decrease with increasing relatedness in the classical optimal skew model.

According to the incomplete control model, both the dominant and the subordinate will exert decreasing effort (e.g., aggression) to enhance their shares of group reproduction, as their relatedness increases. At all values of r, the subordinate's effort will exceed that of the dominant. In contrast, in the classical skew models, increased relatedness will increase the skew. This in turn will increase the payoffs both for the subordinate's aggressive testing of dominants and for the dominant's advertisement of its alpha status. Aggression by both parties is therefore predicted to be higher with closer kinship in the optimal skew model (Reeve and Keller, 1997; Reeve and Ratnieks, 1993).

In the incomplete control model, ecological constraints affecting x do not influence the partitioning of reproduction (except through correlation with the parameters r and k), whereas in the classical optimal skew model the subordinate's share of reproduction decreases as x decreases (i.e., as ecological constraints increase; Equation 3). A closely related theoretical result is that the subordinate's share of reproduction in the incomplete control model will often markedly exceed that specified by the classical optimal skew model when relatedness is symmetrical (Figure 3).

Asymmetrical relatedness (parent–offspring associations). When a subordinate offspring is present in a group with a dominant parent and any mixture of full-sibling and unrelated subordinates, the subordinate is predicted to exert zero effort and thus obtain no direct reproduction in the incomplete control model (in the absence of inbreeding; appendix). In contrast, the subordinate offspring can receive reproduction in the optimal skew model, but only if such groups

Table 2

Degree of reproductive skew in cooperatively breeding birds in relation to relatedness between potential co-breeders

Relatedness between potential co-breeders	Reproductive skew[a]		Reference
	Females	Males	
Intraspecific comparisons			
Gallinula chloropus (common gallinule)			
High (mother–daughter nests)	61%[1]	NA	
Low (unrelated female nests)	49%*	NA	McRae (1996)
Porphyrio porphyrio (pukeko)			
High (Shakespear: North island)	0.17[2]	0.39[2]	
Low (Otokia: South island)	0.04*	0.25	Jamieson (1997)
Merops bullockoides (white-fronted bee-eater)			
Average r of beta male to dominant pair			
High ($r = 0.5$)	NA	36%[3]	
Moderate ($r = 0.25$)	NA	18%	
Low ($r < 0.25$)	NA	0%*	Emlen and Wrege (1992)
Nesomimis galapagoensis (Galapagos mockingbird)			
Higher (Champion Island)	90%[4]	NA	Curry (1989)
Lower (Genovesa Island)	48%	NA	Curry and Grant (1990)
Acrocephalus sechellensis (Seychelles' warbler)			
Higher (Cousin island)	55%[5]	NA	
Lower (Aride island)	Lower	NA	J. Komdeur (personal communication)
Interspecific comparisons: congeneric			
Aphelocoma coerulescens vs. *A. ultramarina* (Florida vs. Mexican jay)			
Higher (coerulescens)	100%[6]	NA	Woolfenden and Fitzpatrick (1984)
Lower (ultramarina)	63%	NA	Brown (1986)
Calocitta colliei vs. *C. formosa* (black-throated vs. white-throated magpie jay)			
Higher (colliei)	89%[4]	NA	Winterstein (1985)
Lower (formosa)	80%	NA	Innes (1992)
Intergeneric comparisons			
Tribonyx mortieri vs. *Gallinula tenebrosa* (Tasmanian hen vs. Dusky moorhen)			
High (*T. mortieri*)	100%[7]	83%[7]	Gibbs et al. (1994)
Low (*G. tenebrosa*)	Low[8]	Low[8]	Garnett (1980)
Parabuteo unicinctus vs. *Buteo galapagoensis* (Harris' hawk vs. Galapagos hawk)			
High (*P. unicinctus*)	NA	100%[9]	Faaborgh and Bednarz (1990)
Low (*B. galapagoensis*)	NA	60%[7]	Faaborgh et al. (1995)

[a] Method of estimating skew: [1]% of incubated eggs at joint nests with two females present that were laid by the dominant female; [2] skew calculated by method of Pamilio and Crozier (1996); [3]% of mated subordinates whose prebreeding or breeding activities were disrupted by the dominant pair; [4]% of reproductive events in groups with >1 female in which the dominant female is the breeder; [5]% of eggs laid in groups with >1 female which are laid by the dominant female; [6]% of successful nestings in groups with >1 female in which the dominant female is the breeder; [7]% of young hatched from nests with >1 potential breeder that were produced by the dominant (as determined by DNA fingerprinting); [8]based on statements that: "all males copulated with all females," "no differences in sexual success between individual birds were detected," and "where one group contains two females, both lay in the same nest" (Garnett, 1980: 103, 108, 110; [9]based on electrophoretic analysis of 4 young, plus intensive observations showing that all copulations involved the dominant male, and subordinate males "showed no interest in copulating." Asterisk (*) denotes significant within-pair difference at the $p < .05$ level.

contain at least one same-sex subordinate in addition to the parent and the offspring. Thus, all else being equal, the occurrence of subordinate reproduction in asymmetric parent–offspring groupings is more consistent with the optimal skew than with the incomplete control model.

High levels of aggressive testing by subordinates and of assertion of status by dominants are not predicted by either model, but for parent–offspring associations larger than dyads, aggression is predicted to be higher by the optimal skew than by the incomplete control model. This difference arises because, for such groups, the genetic interest of the subordinate offspring is the same as that of the dominant parent in the incomplete control model, but it is not the same in the optimal skew model, as indicated by the fact that the dominant parent must yield staying incentives to subordinate offspring under a wide range of conditions (Equation 9).

In the incomplete control model, the degree of skew will be largely unaffected by the magnitude of ecological constraints affecting x. Optimal skew models make the same prediction, but only for the restricted case of dyadic associations. In larger parent-offspring associations, ecological constraints can affect skew, with the subordinate's share of reproduction again decreasing as x decreases (Equation 9).

We next examine data drawn from both vertebrate and hymenopteran societies that address these predictions.

Review of the available evidence

Reproductive skew as a function of relatedness

Sufficient data are available from long-term studies of cooperatively breeding birds to allow a preliminary test of the models. Using a pairwise comparisons test to control for differences in phylogeny (Møller and Birkhead, 1992), both intraspecific and interspecific comparisons support the classical, optimal skew prediction that dominants obtain a greater share of the reproduction as the relatedness between dominants and subordinates increases (Table 2). A sign test across comparisons reveals a significant tendency for skews in groups with high relatedness to exceed those in groups with low relatedness (intraspecific comparisons, $n = 6$, $p = .016$; interspecific comparisons, $n = 5$; $p = .03$).

Superficially, these data support the optimal skew, not the

incomplete control, predictions. However, many of the comparisons are between groups of parents and offspring (possibly asymmetrical relatedness) and groups of unrelated individuals (symmetrical relatedness) and could still be consistent with the incomplete control models because the latter, like optimal skew theory, predicts relatively high skews in dominant parent–subordinate offspring associations (appendix). These cases require further analysis. Below we examine three cases in detail.

Among common moorhens (*Gallinula chloropus*), two females often lay eggs communally in the same nest. When this occurs, the second female may be either an unrelated adult or a grown daughter of the senior female. McRae (1996) calculated the proportion of eggs belonging to the senior female as a measure of skew. This proportion was significantly greater when the junior female was her daughter than when the females were unrelated, results that McRae (1996) interpreted as supportive of optimal skew theory. However, McRae further reported that in all cases where junior females were daughters, they mated incestuously with their fathers. In this specific case of inbreeding, the daughter's effective relatedness to the mother is likely to be greater than the reverse relatedness (r_i = ⅔ and ½, respectively, as defined for Equation 8), and thus the incomplete control model can also explain the higher skew in the parent–offspring groups (i.e., the dominant's effort relative to the subordinate's effort is higher in the parent–offspring groups).

Pukeko (*Porphyrio porphyrio*) are communally breeding gallinules that form mate-sharing groups of one to four males and one to two females. A single nest is built, and most adults assist in rearing the young. Jamieson (1997) reported large geographic variation in the social organization of this species in New Zealand. On North Island, breeding groups are composed of close kin (offspring are retained to form families), while on South Island they are composed of unrelated coalitions of adults. As with moorhens, incestuous matings were common on North Island, but the inbreeding involves both parent–offspring and sib–sib matings (Craig and Jamieson, 1988). In this case, the mean effective relatedness between dominant and subordinate may be nearly symmetrical, depending on the frequencies of the kinds of inbreeding: (1) if subordinates mate with the controlling (i.e., skew-determining) parent, effective relatedness can be symmetrical; (2) if subordinates mate with the noncontrolling parent, there can be an asymmetry in which the subordinate's effective relatedness is greater (as in moorhens); and (3) if subordinates mate with siblings, there can be an asymmetry in which the dominant's effective relatedness is greater. DNA fingerprinting has shown that reproductive skew is greater for both sexes on North Island, where the subordinates typically are offspring of a dominant pair. This finding appears to support the optimal skew model predictions given the likelihood of an overall nearly symmetrical relatedness (Jamieson, 1997).

White-fronted bee-eaters (*Merops bullockoides*) live in socially monogamous, extended family groupings in which multiple pairs may reproduce simultaneously. Different family members "disagree" over reproduction, however, with dominants sometimes actively disrupting the prebreeding or breeding activities of subordinates. Although this at first sounds like a tug-of-war, it follows the prediction of optimal skew theory. Examining only cases of symmetrical relatedness (parent+step-parent–offspring, brother–brother, lesser nondescendent kin-ego, and nonkin–nonkin), the likelihood of subordinate breeding increases as relatedness to the dominant(s) decreases (data from Emlen and Wrege, 1992).

Three other cases of egalitarian breeding have been reported among cooperatively breeding birds. These are Galapagos hawks (*Buteo galapagoensis*), groove-billed anis (*Crotophaga sulcirostris*), and guira cuckoos (*Guira guira*). In each, the multiple breeders have been found to be unrelated individuals (Faaborg et al., 1995; Koford et al., 1990; Quinn et al., 1994). This association broadly supports the optimal skew models because if the incomplete control models were largely correct, we should be just as likely (or more likely) to find egalitarian reproduction among symmetrically related kin such as siblings as among non-kin.

Among mammals, two studies provide more support for the optimal skew models. Dwarf mongooses (*Helogale parvula*) live in groups of 8–18 individuals. A dominant "pair" typically monopolizes reproduction, but 13% of subordinate females produce litters and 24% of young are sired by subordinate males. For both sexes, there are numerous subordinates present in the group, but the few that reproduce are those least related to the dominants; moreover, the amount of reproduction they receive appears close to the theoretical staying incentive of the optimal skew model (Creel and Waser, 1991; Keane et al., 1994). Among male lions (*Panthera leo*), reproduction is also shared more equitably when groups are composed of unrelated individuals than when they consist of siblings (i.e., symmetrically related kin; Packer et al., 1991).

Data from social insects also provide support for the optimal skew models. As reviewed by Keller and Reeve (1994), unrelated ant foundress queens appear to divide reproduction equitably, in contrast to associations of closely and symmetrically related wasp queens, among which reproduction typically is greatly skewed in favor of a single dominant female. Recent genetic data on the communal bees *Perdita texana* and *Andrena jacobi* also showed that nest-mate queens are only distantly related and, as predicted by optimal skew models, they do contribute relatively equally to reproduction (Danforth et al., 1996; Paxton et al., 1996). An intrageneric comparison (Reeve 1991) also hints at an association between the degree of reproductive skew and relatedness in the genus *Polistes*, with lower-skew societies being composed of symmetrically related queens of lower relatedness.

Evidence for a relationship between reproductive skew and relatedness among queens also comes from intergeneric and intrageneric comparisons among ants. Intergeneric data on both reproductive skew and relatedness from the same populations are available for four species (Table 3). Among these species there is a perfect rank correlation between reproductive skew and genetic relatedness, with skew increasing as relatedness increases. The association of high skew with high relatedness is exhibited even between different populations of the same species of *Leptothorax acervorum* (Bourke et al., 1997). These data can be reconciled with the incomplete control models only if the higher-skew societies have higher proportions of queens that are offspring (asymmetrically related) to the dominant queen.

The same positive association between queen–queen relatedness and reproductive skew was found in an intrageneric comparison within the ant genus *Leptothorax*. In some *Leptothorax* species, all queens contribute to reproduction (polygyny), whereas in some others a single queen monopolizes all of the reproduction (functional monogyny). As predicted by optimal skew models, the relatedness among nest-mate queens is higher in the functionally monogynous species (high skew) than in the five polygynous species (lower skew) (Table 4). Taken together, these data are most consistent with high skew being associated with high relatedness in ants. However, caution is necessary because data are available for only a few species, and the possibility and extent of asymmetric relatedness between subordinates and dominants, particularly in the functionally monogynous species, has yet to be investigated. Moreover, there is a negative correlation between queen–queen relatedness and queen number in ants (Keller,

Table 3
Reproductive skew and relatedness in ants

Species	Skew	Measure	Reference	Relatedness	Reference
Linepithema humile (previously *Iridomyrmex humilis*)	0.02	Egg-laying rates	Keller (1988, unpublished data)	0.03	Kaufmann et al. (1992)
Solenopsis invicta	0.09	Parentage of workers	Ross (1988)	0.08	Ross (1993)
Leptothorax acervorum	0.12	Egg-laying rates	Bourke and Franks (1995)	0.26	Heinze et al. (1995)
	0.42	Parentage of workers	Bourke et al. (1997)	0.48	Bourke et al. (1997)
Leptothorax gredleri	1.00	Egg-laying rates	Bourke and Franks (1995)	0.60	Heinze (1995)

We considered only species for which data on reproductive skew and queen–queen relatedness were obtained from the same population. Relatedness among queens may vary greatly among populations (see Keller, 1995), and it is unknown whether such differences may correlate with differences in reproductive skew.

1995), so that variation in queen number might be a confounding variable influencing skew independently of relatedness. Finally, as Heinze (1995) pointed out, high relatedness among queens within colonies might result from high skew (rather than the reverse) when queens are readopted into their native colony, as indeed is probably the case in many polygynous ant species (Chapuisat et al., 1997; Keller, 1995; Stille and Stille, 1992; Stuart et al., 1993). For such species, additional studies are needed to uncover the causal role of relatedness in the evolution of skew.

Intragroup aggression as a function of relatedness

Few studies of cooperatively breeding vertebrates have examined intragroup aggression in detail. Jamieson (1997) found that groups of communally breeding pukeko with higher intragroup relatedness (and higher skews) exhibited higher levels of within-group aggression, in strong accordance with optimal skew, and not incomplete control, models. Emlen and Wrege (1992) also reported the greatest harrassment levels between the most closely related pairs in white-fronted bee-eater families. Similarly, colonies of the naked mole rat (*Heterocephalus glaber*), the vertebrate society exhibiting the highest known worker–breeder relatedness ($r = 0.81$, due to extensive inbreeding; Reeve et al., 1990) also exhibit an extremely high skew for both males and females (Sherman et al., 1991) and frequent, often intense, intracolony aggression (e.g., Reeve, 1992).

As reviewed by Keller and Reeve (1994), unrelated ant foundress queens fail to display dominance behavior, in vivid contrast to associations of closely related wasps queens in which skews are higher and dominance behavior can be intense. Moreover, intracolony aggression positively correlates with both skew and aggression across multiple-queen leptothoracine ant species (Bourke and Heinze, 1994). Overall, the few data on the relationships among relatedness, skew, and aggression clearly favor the optimal skew models.

Table 4
Reproductive skew in polygynous (shared reproduction) and monogynous (monopolized reproduction) multiqueen colonies of leptothoracine ants

Species	Relatedness
Polygynous	
Leptothorax canadensis	0.56
Leptothorax acervorum	0.50
Leptothorax muscorum	0.19
Leptothorax ambiguus	0.34
Leptothorax longispinosus	0.51
Functionally monogynous	
Leptothorax gredleri	0.60

Data from Heinze (1995).

Reproductive skew as a function of ecological constraints on independent breeding

The classical skew model predicts that reproductive skew should increase with decreasing expected success of independent breeding (low x), whereas the incomplete control model predicts no such direct connection. In a remarkable study, Bourke and Heinze (1994) investigated the factors underlying variation in reproduction among nest-mate queens in the tribe Leptothoracini, a group of ants particularly suitable for such studies because of their extreme diversity in social organization. They found that the degree of reproductive skew increases with greater ecological constraints on dispersal, as predicted by optimal skew models. Peters et al. (1995) showed that reproductive dominance tends to increase over time in queen associations in the social wasp *Polistes annularis*, a result that supports the classical skew prediction if, as seems likely, ecological constraints on independent nesting increase as the colony cycle progresses (Reeve, 1991).

Among vertebrates, we know of data for only three avian species, the pukeko, the white-fronted bee-eater, and the Galapagos mockingbird (*Nesomimus parvulus*). In the first, skew was much greater at Shakespear (North Island) where ecological constraints were severe than at Otokia (South Island) where they were weak (Jamieson, 1997). In the latter two, skew varied between years, being lowest in years when ecological conditions were most benign (Emlen, 1982a; Curry, 1988). Clearly, much more data are required to test these predictions for both vertebrate and invertebrate societies.

DISCUSSION

Reproductive skew models (or "concession models" as recently termed by Clutton-Brock, in press) have generated considerable interest recently on both theoretical and empirical levels. However, rigorous testing of optimal skew models has been hampered by the lack of any formal alternatives. The two incomplete control models developed here represent clear-cut and testable alternatives.

In classical optimal skew models, a basic assumption is that the dominant individual controls the distribution of reproduction in a group. Shared reproduction, when it occurs, results from the dominant yielding (conceding) just enough reproduction to subordinates to make it favorable for the latter to remain in the group and cooperate peacefully. In the incomplete control models, this assumption is relaxed and dominant and subordinate directly compete to increase their respective fractions of the total reproduction. Shared reproduction in these models results from the inability of the dominant to profitably monopolize the group's reproduction. The effort

expended in reproductive competition is assumed to entail a cost, however, and that cost is a decrease in total group reproductive output. The incomplete models solve for the optimal amount of effort expended by both participants and allow calculation of the resulting partitioning of reproduction between them.

The two categories of models should be easily distinguishable because they make divergent predictions about the allocation of reproduction in groups. The central prediction of the incomplete control model is that reproductive skew should decrease with, or be insensitive to, increasing genetic relatedness among group members when this relatedness is symmetrical among them. This contrasts with the prediction of classical optimal skew models that reproductive monopolization should increase with increasing relatedness. When relatedness is asymmetrical, as often is the case when subordinate offspring are associated with dominant parents, reproduction by offspring is more likely in the optimal skew models than in the incomplete control models if the group is larger than a dyad and consists of any mixture of full-sibling and unrelated subordinates. Finally, the incomplete control models predict that skew should be insensitive to the magnitude of ecological constraints (the probability of successful dispersal and independent reproduction by the subordinate). In classical skew models, however, the amount of reproduction conceded by the dominant to the subordinate increases with decreasing ecological constraints.

The available data from both vertebrate and hymenopteran societies currently support the classical optimal skew models, but this conclusion remains tentative. Much more genetic and behavioral data are required to adequately test either model.

Unfortunately, the terminology of skew theory has led to misunderstandings about what optimal skew theory assumes and predicts, resulting in some erroneous claims about what kinds of data would reject the theory. For example, the idea of a dominant's "conceding" reproduction in return for favorable actions, in essence the notion of social contracts (Reeve and Nonacs, 1992), may seem to assume a sophisticated, conscious, decision-making process. This is not the case. Selection operating on simple decision rules (behavioral "rules-of-thumb") can often lead to sophisticated, context-dependent behavioral actions (e.g. Dunbar, 1984; Emlen, 1997a; Emlen et al., 1995; Stephens and Krebs, 1986). Complex cognition is not assumed by optimal skew theory. The only requirements are mechanisms for monitoring one's reproduction relative to others, reducing attempted reproduction when the latter exceeds some pre-programmed or movable threshold, and increasing aggression or leaving the group when this relative reproduction falls short of some fixed or flexible threshold. Indeed, the minimal cognitive abilities presupposed by optimal skew theory seem hardly more complex than those assumed by incomplete control theory.

Similarly, the fact that intense aggression and active breeding suppression are observed within groups might mistakenly be taken as evidence refuting models based on reproductive concessions. But again, this need not be so. Accurate assessment of relative status and resource-holding power are assumed and incorporated into optimal skew models as well. In fact, as the reprductive skew increases (all else being equal), skew theory predicts higher levels of testing by subordinates and consequently of demonstration of status by dominants. This is because the payoff for detection of a reversal in fighting ability for the subordinate increases along with the skew (Reeve and Ratnieks, 1993). Aggression is thus expected to be part of the mechanistic process by which the stable partitioning of reproduction is established and maintained in the optimal skew models.

The exchange of "bribes" provides a further illustration of how observed aggression can be fully compatible with optimal skew theory. In a recent extension of optimal skew theory, Reeve and Keller (1997) showed that dominants and subordinates will be favored to yield reproduction to each other ("bribe" each other) to suppress destructive, selfish acts (i.e., acts that reduce overall group output while increasing the actor's share of the reproduction). Thus, aggression within groups may simply be selfish threats performed to secure reproductive bribes (Reeve and Keller, 1997). Moreover, bribing provides a mechanism by which dominants and subordinates can mutually suppress the selfish efforts assumed in the incomplete control models, thus causing the partitioning of reproduction to approach that predicted by the optimal skew models.

Suppose that a dominant is selected to provide a small bribe to a subordinate in addition to the latter's staying incentive. In this case, the subordinate's reproduction would be above the minimum staying incentive, just as in the incomplete control models. However, it will still be true that increasing relatedness will increase the reproductive skew because the magnitudes of bribes (like staying incentives) are predicted to decrease with increasing relatedness (Reeve and Keller, 1997). In other words, since both staying incentives and any added bribes should decrease in magnitude with increasing relatedness, it must be true that the subordinate's total share of the reproduction should decrease with increasing relatedness.

Both bribe and optimal skew models are examples of a transactional paradigm in which dominants yield reproduction to subordinates to reap some benefit (retaining a subordinate, in the case of a staying incentive, or preventing it from engaging in a selfish act destructive to the group, in the case of a bribe). For both models, the amount of a reproductive payment (concession) necessary to induce a subordinate to engage in some behavior beneficial to the dominant will always decrease with increasing relatedness between them.

The relative applicability of optimal skew versus incomplete control models has rather profound implications for our understanding of the evolution of animal societies. If the optimal skew models are correct, the possibility of a truly unified theory of social evolution is greatly enhanced because these models provide a fairly straightforward theoretical apparatus for linking the ecology and genetic structure of societies to their reproductive partitioning and patterns of intragroup conflict. If the incomplete control models are correct, this linkage is largely severed, and the models describing internal social dynamics will have to be decidedly more "local" (i.e., tailored quite differently to different social systems).

Even more fundamentally, the two different kinds of models entail different views about the degree of sophistication in interactions between members of an animal society. In the incomplete control model, interactants are engaged in a tug-of-war struggle over resources, but in the optimal skew and bribe models, organisms are engaged in higher-order transactions—exchanges of parcels of reproduction designed to induce recipients to behave in a more favorable way. It is of fundamental importance to determine if the latter transactional view applies outside of humans, not only to nonhuman vertebrate societies but also to invertebrate societies. If so, the implication will be that we have previously underestimated the power of selection to design social behaviors of considerable intricacy and subtlety in the absence of cognitive complexity.

APPENDIX

Why is skew virtually insensitive to relatedness in the subordinate inefficiency model?

The change in the dominant's evolutionarily stable effort with small changes in relatedness is given by $\partial x^*/\partial r$ which is $-(x$

$+ by)/2(1 - r)$. Similarly, $\partial y^*/\partial r$ is $-(x + by)/2b(1 - r)$. These expressions mean (roughly) that y^* changes $1/b$ as fast as x^* for a given change in r; both change in the same direction, but since $b < 1$, y^* will tend to change faster. The dominant's share of reproduction is $x^*/(x^* + by^*)$, which is more sensitive to changes in x^* than y^* because $b < 1$. Thus, although y^* changes faster than x^*, a change in y^* has a lesser effect than a change in x^* on the skew; the net result is virtual insensitivity of the skew to relatedness.

In the incomplete control models, zero reproduction is predicted for subordinate offspring when associated with a singly mated parent (parent and offspring have the same relatednesses to other group members)

Subordinate inefficiency model. Let y be the subordinate offspring's effort (with efficiency b), x be the effort of the singly mated parent (with efficiency d), and z be the summed efforts of the other group members. The offspring has an asymmetrical relatedness of 1 to its parent and 1 to itself. Thus, by Equation 8, the offspring's inclusive fitness can be written as

$$I_s = \left[\frac{rcz + dx + by}{cz + dx + by}\right](1 - x - y - z), \qquad (15)$$

where c represents the combined "efficiency" of the other group members and is equal to $c = [(\Sigma c_i x_i)/(\Sigma x_i)]$ and r is the effective mean relatedness to other group members and is equal to $r = [(\Sigma r_i c_i x_i)/(\Sigma c_i x_i)]$ (these summations over the other group members allow us to collapse all other group members conveniently into a single "individual"). The parent has an asymmetrical relatedness of ½ to its offspring and 1 to itself. We assume that the parent has the same (or lesser) relatedness to other group members as does the offspring. This will be true for most kinds of groups, e.g., groups with a parent and multiple offspring or with a parent and any mixture of offspring and unrelated individuals. (It would *not* be true of a group containing a parent, an offspring, and the offspring's first cousin.) Thus, the parent's inclusive fitness is

$$I_d = \left[\frac{rcz + dx + (1/2)by}{cz + dx + by}\right](1 - x - y - z). \qquad (16)$$

Zero effort and thus zero reproduction by the subordinate will be the evolutionarily stable strategy when $\partial I_s/\partial y_{y=0,x=x^*,z=r^*} < 0$. We thus calculate $\partial I_d/\partial y$ with y set equal to zero and with r set equal to the value for which $\partial I_d/\partial y_{y=0,x=x^*,z=r^*} = 0$ (taking into account the parent's maximization of its own personal reproduction). This yields

$$\frac{\partial I_s}{\partial y_{y=0,x=x^*,z=r^*}} = \frac{-(d - b)(1 - x^* - z^*)}{d(1 - z^*) + cz^*}, \qquad (17)$$

which is negative if the parent
is dominant to the offspring ($d > b$). Thus, the offspring will not exert any effort and will not reproduce under the assumed conditions.

Restricted access model. Using Equation 14 for the inclusive fitnesses, we proceed exactly as above for the subordinate inefficiency model, obtaining $\partial I_s/\partial y_{y=0,x=x^*,z=r^*} = 0$. This means y is at a local maximum at $y = 0$, because it can be shown that $\partial^2 I_s/\partial y^2_{y=0,x=x^*,z=r^*} < 0$. Again, the offspring will not exert any effort and thus will not reproduce under the assumed conditions.

Dominant effort decreases with relatedness when there is constant subordinate effort

Hamilton's rule implies that the optimal level of general effort, e^*, for the dominant will be that which maximizes the inclusive fitness quantity

$$w(e) = [1 - p(e)]k(e) + rp(e)k(e), \qquad (19)$$

where $p(e)$ is the subordinate's fraction of reproduction, which is a decreasing function of the dominant's effort e [i.e., $\partial p(e)/\partial e < 0$] and $k(e)$ is the total group output, which is a decreasing function of e [i.e., $\partial k(e)/\partial e < 0$]. By the implicit function theorem of calculus, the rate of change of the dominant's optimal effort, e^* with relatedness is

$$\partial e^*/\partial r = -\frac{p(e)\dfrac{\partial k(e)}{\partial e} + k(e)\dfrac{\partial p(e)}{\partial e}}{\partial^2 w(e)/\partial e^2} \quad \text{at } e = e^* \qquad (20)$$

If the dominant's optimal effort corresponds to an internal inclusive fitness maximum (i.e. an intermediate peak in inclusive fitness, since we assume in the incomplete control model that the dominant is favored to exert a less-than-maximal effort), then the denominator is negative. The numerator also must be negative given that $\partial p(e)/\partial e < 0$ and $\partial k(e)/\partial e < 0$, so it follows that $\partial e^*/\partial r$ must be negative (i.e., the dominant's optimal effort and thus the skew should decrease with increasing relatedness).

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