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Costly young and reproductive skew in animal societies

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Many recent models of reproductive skew explain subordinate reproduction as a staying incentive offered by dominants, who can produce more young with a helper present than without. Here, we present a new, alternative explanation for subordinate reproduction, which applies whenever the fitness cost to a parent of producing young is an accelerating function of the number produced (as commonly assumed in optimal clutch size theory). Under these circumstances, a dominant individual may be selected to offer a share of reproduction to a related subordinate, not as an incentive to stay, but because additional offspring that would be expensive for the dominant to produce are cheap for the subordinate. ''Beneficial sharing'' of this kind is more likely the more closely related the subordinate is to the dominant, so that the model predicts a negative relationship between skew and relatedness. This result runs directly counter to the positive relationship predicted by previous incentive-based models. We explore the interaction of these contrasting effects by developing an integrated model that allows for both beneficial sharing and staying incentives. When offspring are cheap to produce, this integrated model predicts that the incentive effect will dominate, and skew will increase with relatedness. When young are costly, in contrast, beneficial sharing will be of greater importance, and skew will decrease with relatedness. *Key words:* cooperative breeding, cost of reproduction, dominance, reproductive skew, subordinate. *[Behav Ecol 10:178–184 (1999)]*

A current focus of behavioral ecology is to identify what factors determine the distribution of reproduction, or the degree of reproductive skew, in social groups. In high-skew animal societies, one or a few individuals monopolize reproduction, whereas in low-skew societies breeding is distributed more equally (Keller and Reeve, 1994; Vehrencamp, 1983a,b). The level of reproductive skew varies widely, even between closely related species. For example, in dwarf mongooses (*Helogale parvula*) usually only one female breeds (Creel and Waser, 1991; Keane et al., 1994; Rood, 1990), whereas in banded mongooses (*Mungos mungo*) it is the norm for all adult females in the group to give birth together (Rood, 1975; Cant M, unpublished data). Similarly, in social insects there is often great variety within genera in the number and relative contribution of queens to colony reproduction (Keller and Vargo, 1993; Spradberry, 1991).

Vehrencamp (1979, 1983a,b) introduced a simple optimal skew model to explain the division of reproduction in groups of cooperative breeders. This and extended versions of the model (e.g., Johnstone et al., in press; Reeve, 1998; Reeve and Keller, 1995; Reeve and Ratnieks, 1993) make the assumption that the distribution of reproduction within a group is under the control of a single dominant animal. The dominant offers reproductive ''staying incentives'' to subordinates who might otherwise do better to leave, perhaps because they have a high chance of dispersing successfully or because they are unrelated to the dominant's young and therefore accrue no indirect fitness benefit by helping her to raise offspring. Thus, incentive-based models predict that high skew will be associated with severe ecological constraints on independent breeding and high relatedness between group members.

Incentive-based models of skew have generated a great deal of interest because they potentially provide a framework to account for variation in skew across all sorts of taxa, from social insects to communally breeding mammals (see Keller and Reeve, 1994; Reeve et al., 1998). Moreover, there is some empirical support for their predictions. For instance, in leptothoracine ants high skew is found associated with strong ecological constraints, and possibly with high relatedness, although data regarding the latter are scarce (Bourke, 1997; Bourke and Heinze, 1994; Heinze, 1995). Similar associations have also been reported in a few vertebrate species (reviewed by Emlen, 1997). Clutton-Brock (1998), however, points out that few of these vertebrate studies are able to rule out alternative explanations for the observed patterns of skew and concludes that there is a need for more sophisticated models. This is particularly the case if we expect the models to be applicable to social organisms with radically different biology.

Here, we develop a new optimal skew model that incorporates a hitherto neglected factor, the cost of producing young. This cost is of great importance because it can potentially provide a novel explanation for subordinate reproduction. When, as commonly assumed in classical optimal clutch size models (e.g., Charnov and Krebs, 1974; Daan et al., 1990; Kacelnik, 1989; Trivers, 1972, 1974), it becomes increasingly costly for a dominant individual to add each successive offspring to a brood, it may pay to yield a share of reproduction to a related subordinate, even if the latter does not help with offspring care (following Trivers, 1972, we define cost in terms of the decrement to the future reproductive value of the parent). This is because additional offspring would be expensive for the dominant to produce but are cheap for the subordinate. Previous models of reproductive skew have not explicitly dealt with the costs of offspring production (e.g., Reeve and Ratnieks, 1993) or else have assumed that such costs are linear (Johnstone and Cant, in press) and thus have overlooked this possibility.

To explore the consequences of accelerating costs of producing young on the stable partitioning of reproduction, we first consider the simplest possible case in which a subordinate must remain in association with the dominant but contributes nothing to offspring care. Under these circumstances, the dominant will never offer a staying incentive and will only give up a share of reproduction as a means of defraying the costs of offspring production. We then integrate this approach with

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existing incentive-based models by incorporating a subordinate contribution to care and allowing the subordinate the decision of whether to disperse or to stay and help in an association with the dominant. We show that the predictions of this integrated model are highly sensitive to the magnitude of the cost of young. Consequently, we suggest that patterns of skew are likely to differ markedly between the societies of insects, birds, and mammals because the costs of offspring production differ markedly among these different taxa.

The model

A basic model incorporating accelerating costs of young

We consider a situation where offspring fitness depends on brood size and ask how reproduction will be shared between two females, referred to as Alpha and Beta, who contribute to a communal brood. Alpha is dominant to Beta and has full control over the distribution of reproduction. She produces n young herself and allows Beta to produce f young. The total brood size is denoted t $(=n + f)$.

For simplicity we assume that individual offspring fitness, $s(t)$, declines linearly with brood size, t, so that $s(t) = 1 - kt$, where k is a measure of the sensitivity of offspring to increasing brood size (the results are qualitatively similar for a nonlinear decrease in offspring fitness with brood size). The total productivity of a brood of size t is given by

$$T(t) = t(1 - kt). \tag{1}$$

Producing young entails an accelerating fitness cost (sensu Trivers, 1972) to the individual parent. To be more precise, we assume that the cost of producing n young is equal to xn^2, where x is some constant (we use this particular function for reasons of tractability; other accelerating functions yield qualitatively similar results). Note that we are concerned with personal costs incurred solely by the breeder that produces the n offspring, rather than shared costs involved in rearing young to independence.

We can readily find the optimum clutch size for a single breeder: this will be the brood size that maximizes $F(n)$, the net benefit of producing n young. $F(n)$ is given by

$$F(n) = n(1 - kn) - xn^2$$

Solving for n, a single female's optimum clutch size, we obtain

$$\hat{n} = \frac{1}{2(k + x)} \tag{2}$$

(see Figure 1).

To analyze what happens when two females contribute to the brood, we find an expression for the inclusive fitness payoff to Alpha as a function of n and f. Because in this model Alpha has full control over the distribution of reproduction, the evolutionarily stable individual brood sizes n^* and f^* are those for which Alpha's inclusive fitness payoff from the breeding attempt is maximized.

Assuming that the total productivity of a combined brood, $T(n + f)$, is shared according to the relative contributions of the two breeders, we can write Alpha's inclusive fitness payoff, w_α, as follows:

$$w_\alpha = \frac{n}{n + f} T(n + f) - xn^2 + r\left[\frac{f}{n + f} T(n + f) - xf^2\right].$$

The first two terms on the right-hand side of this expression represent Alpha's direct fitness payoff, the term in brackets represents Beta's direct fitness payoff, and r is the coefficient of relatedness between Alpha and Beta.

Rearranging we obtain:

$$w_\alpha = (n + rf)[1 - k(n + f)] - x(n^2 + rf^2). \tag{3}$$

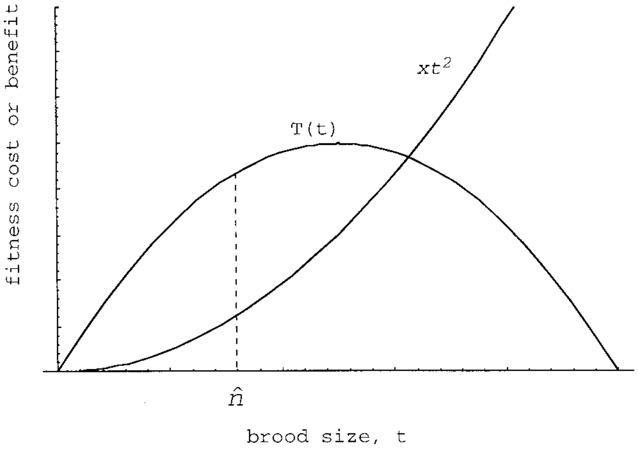

Figure 1
Fitness costs (xt^2) and benefits $[T(t)]$ of reproduction as a function of brood size (t), for a single breeder; x is the relative cost of young. The optimum brood size, $\hat{n}$, is that which maximizes the net benefit of producing young.

To find n^* and f^* we calculate the partial derivatives of w_α with respect to n and to f, set both equal to zero, and then solve simultaneously for n and f. The solution is

$$n^* = \frac{r(kr - 2x - k)}{k^2(1 - r) - 4r(2kx + x^2)} \tag{4a}$$

$$f^* = \frac{k - r(k + 2x)}{k^2(1 + r)^2 - 4r(k + x)^2} \tag{4b}$$

(it is easy to show that these are fitness maxima). This solution, however, is biologically meaningful only if $f^* \geq 0$ and $n^* \geq 0$. For

$$r < \frac{k}{k + 2x}$$

this requirement is not met, indicating that Alpha does best not to allow Beta any direct reproduction. Under these circumstances, $f^* = 0$ and n^* is equal to a single female's optimal clutch size, given in Equation 2.

Results of the basic model

In a previous model (Cant, 1998) that assumed linear costs of producing young, it never paid Alpha to allow any subordinate reproduction: if there was any benefit to having extra young in the brood, Alpha did better to produce them herself. However, when the cost of producing young is an accelerating function of number produced, additional offspring are expensive for Alpha, while Beta can produce her first few young at relatively low cost. If the two breeders are related, Alpha's payoff can thus be maximized by allowing Beta some share of reproduction (this argument will hold for postproduction costs associated with rearing young to independence only in cases where each parent cares disproportionately for its own young).

The basic model predicts that when relatedness is zero, Alpha never shares reproduction with Beta. When Alpha and Beta are related, Alpha grants a larger share of reproduction to Beta the higher the cost of young (Figure 2). We can summarize this trend using Pamilo and Crozier's (1996) index of skew (S):

$$S = (N_T - Q_E)/(N_T - 1),$$

where N_T is the total number of potential breeders, and Q_E

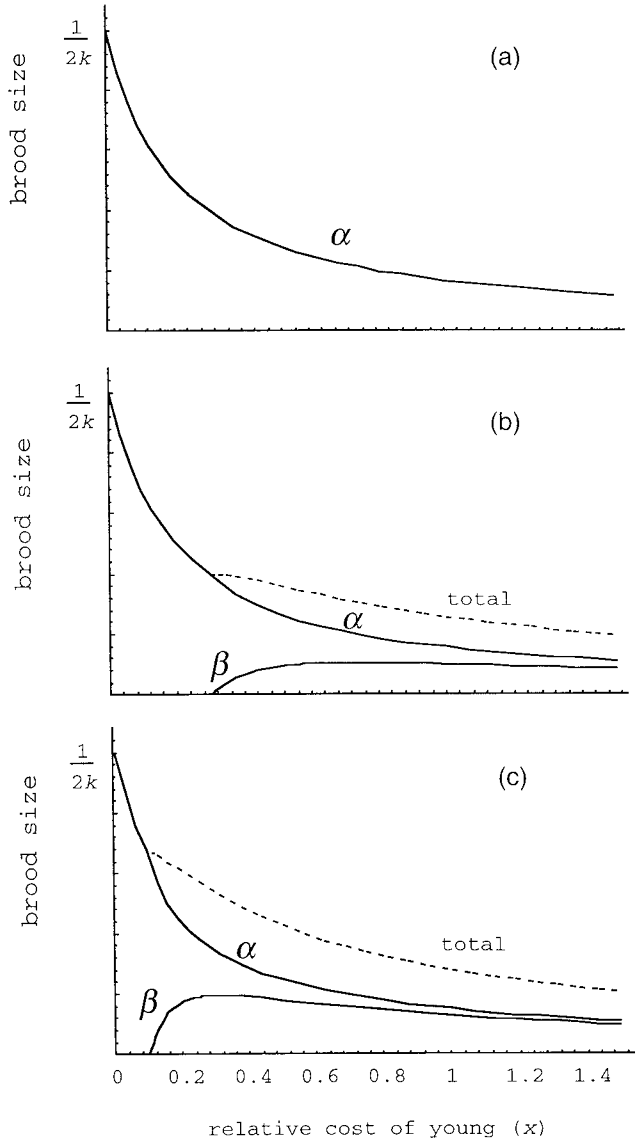

Figure 2
Number of offspring produced by Alpha and Beta in the basic model, as a function of the relative cost of young, *x,* for three values of relatedness between Alpha and Beta: (a) $r = 0$; (b) $r = 0.25$; (c) $r = 0.5$. Also shown is total combined brood size; $k = 0.2$ in all three cases. At higher levels of cost and relatedness, reproduction is shared more equally between the two females.

is the effective number of breeders, defined as $Q_E = 1/\Sigma p_i^2$, where p_i is the reproductive contribution of the ith breeder. As shown in Figure 3, the stable level of skew falls rapidly from 1 (monopolization by Alpha) at low levels of relatedness, to 0 (equal sharing of reproduction) at $r = 1$. The threshold value of relatedness above which this decline begins is lower the higher the cost of young (Figure 3). This predicted relationship between relatedness and skew runs directly counter to previous skew models (e.g., Cant, 1998; Reeve and Ratnieks, 1993).

An integrated model: incorporating options for the subordinate

So far, we have analyzed the stable level of skew as if Beta had no option but to produce the number of young, f^*, permitted by Alpha. In contrast, optimal skew models (e.g., Reeve and Ratnieks, 1993; Vehrencamp, 1983a,b) make two important assumptions concerning the options available to subordinates. First, subordinates may choose to leave the group and have some probability of dispersing successfully to become an independent breeder. Second, two-female associations are more successful in raising young, so subordinates can accrue some indirect fitness benefits from remaining with the dominant. This helping effect is the reason the dominant is willing to offer a reproductive staying incentive to keep the subordinate in the group.

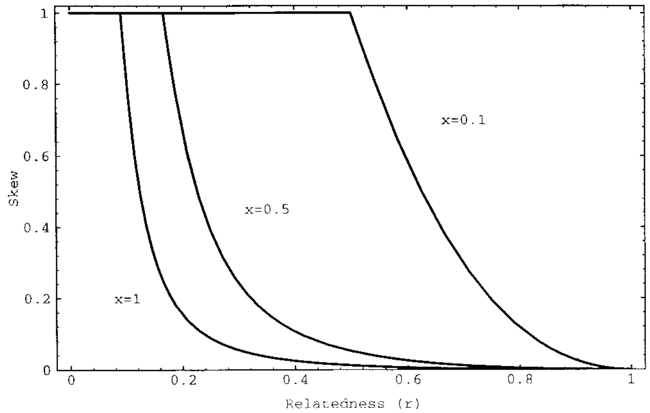

Figure 3
Reproductive skew in the basic model, measured by Pamilo and Crozier's (1996) index *S* (defined in text), as a function of relatedness, for three values of *x,* the cost of young; $k = 0.2$.

We integrate the current model with the models of Reeve and his co-workers (Reeve, 1991; Reeve and Keller, 1995; Reeve and Ratnieks, 1993) by incorporating two additional variables: *d,* the probability with which a subordinate disperses successfully ($0 < d < 1$); and *h,* the ratio of offspring fitness in a two-female association relative to that for a single breeder ($h \geq 1$). The integrated model is then analyzed as follows:

(1) We determine (as above) the optimum numbers of young that Alpha should produce herself, and that she should allow Beta to produce, n^* and f^* (these are the numbers that maximize Alpha's inclusive fitness, taking into account the increased fitness of offspring in a two-member group).
(2) If this division of reproduction results in a higher inclusive fitness payoff for Beta than she would gain by dispersing, then she will remain in the group, and the results of the model are unaffected by incorporating the possibility of dispersal.
(3) If, in contrast, Beta would do better to disperse than to accept the f^* young allowed her by Alpha, we now find an expression for the minimum number of young Alpha must allocate to ensure that Beta would do better to stay in the group. This is equivalent to the staying incentive of Reeve and Ratnieks (1993), though here it is a function of the number of young produced by Alpha.
(4) We find the optimum brood size for Alpha to produce, n_1^*, given that if she produces n young, she must grant at least $f_1^*(n)$ to Beta.
(5) Finally, we check whether it pays Alpha to grant Beta her staying incentive [i.e., to produce n_1^* young herself, and allow Beta to produce $f_1^*(n)$] or whether she would do better to allow Beta to disperse and breed alone.

To find $f_1^*(n)$, the minimum number of young Alpha must allocate to ensure that Beta does better to stay in the group,

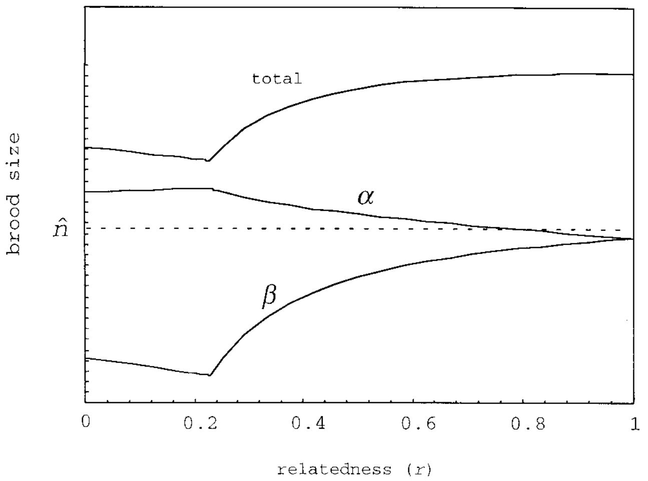

Figure 4
Brood size of Alpha and Beta in the integrated model as a function of relatedness. Also shown is the total brood size. For low values of relatedness ($r < 0.2$), the number offspring produced by Beta declines with relatedness. Above $r = 0.2$, however, Beta's production of young increases sharply while Alpha's declines, until Alpha and Beta share reproduction equally at $r = 1$; $k = 0.2$, $h = 1.5$, $d = 0.6$.

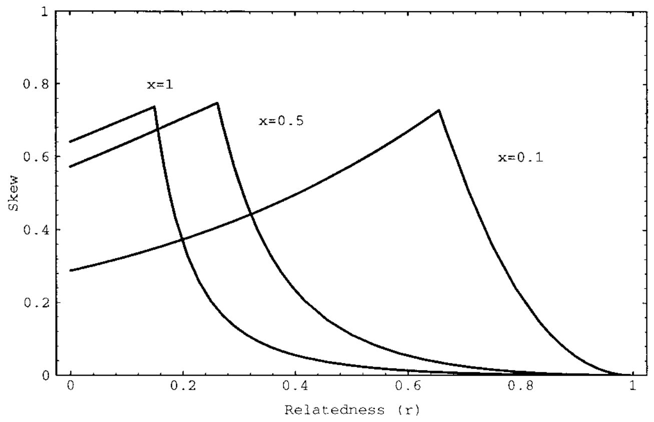

Figure 5
Reproductive skew in the integrated model, measured by Pamilo and Crozier's (1996) index S (defined in text), as a function of relatedness, for three values of x, the cost of young; $k = 0.2$, $h = 1.5$, $d = 0.6$.

we proceed as follows: Let $w_{\beta D}$ equal the inclusive fitness payoff to Beta if she disperses to breed independently, and $w_{\beta S}$ equal her payoff if she stays to help Alpha. If we assume that Beta enjoys the same reproductive success when breeding alone as would Alpha, we can write:

$$w_{\beta D} = d[\text{Beta's payoff when a single breeder}] + r[\text{Alpha's payoff when a single breeder}]$$

or

$$w_{\beta D} = d[\hat{n}(1 - k\hat{n}) - x\hat{n}^2] + r[\hat{n}(1 - k\hat{n}) - x\hat{n}^2],$$

where $\hat{n}$ is given by (2). Similarly, we can write:

$$w_{\beta S} = [\text{Beta's direct fitness in an association}] + r[\text{Alpha's direct fitness in an association}]$$

or

$$w_{\beta S} = h\frac{f}{n + f}T(n + f) - xf^2 + r\left[h\frac{n}{n + f}T(n + f) - xn^2\right],$$

which simplifies to

$$w_{\beta S} = h\{(rn + f)[1 - k(n + f)]\} - x(rn^2 + f^2).$$

Beta's critical share of reproduction as a function of n, $f_1^*(n)$, is found by setting $w_{\beta S} = w_{\beta D}$ and solving for f.

Having obtained an expression for $f_1^*(n)$, we can find the optimum number of young for Alpha to produce given that if she produces n young, she must grant at least $f_1^*(n)$, to Beta. Alpha's inclusive fitness for any n, f is given by

$$w_\alpha = h\{(n + rf)[1 - k(n + f)]\} - x(n^2 + rf^2) \quad (5)$$

To find Alpha's optimum number of young, we replace f in Equation 5 with the derived expression for $f_1^*(n)$, and solve for $dw_\alpha/dn = 0$.

The variables n_1^* and $f_1^*(n_1^*)$ specify Alpha's optimum distribution of reproduction, given that she must allow Beta enough young to keep her in the association. However, we have yet to test whether it pays Alpha to offer a staying incentive, or whether she would do better if Beta dispersed. Thus the solutions n_1^* and $f_1^*(n_1^*)$ are evolutionarily stable solutions only for $w_\alpha^* > w_1$, where w_α^* is the expression obtained after substituting n_1^* and $f_1^*(n_1^*)$ in Equation 5, and w_1 is Alpha's inclusive fitness when Beta disperses, given by

$$w_1 = \hat{n}(1 - k\hat{n}) - x\hat{n}^2 + rd[\hat{n}(1 - k\hat{n}) - x\hat{n}^2]$$

If $w_\alpha^* > w_1$, the evolutionarily stable solution is for Beta to disperse and for both breeders to produce $\hat{n}$ young.

Results of the integrated model

Considering the effect of relatedness on the division of reproduction, we find that initially, as relatedness increases, the number of young produced by Beta declines (Figure 4). This is essentially the effect reported by Reeve (1991) and Reeve and Ratnieks (1993): with increasing relatedness, the size of the staying incentive required to keep the subordinate as a helper declines (here we call this the "incentive effect"). However, above a certain threshold value of relatedness (around $r = 0.2$ in the example shown), this trend is reversed: Beta starts to produce more young, while the number of young produced by Alpha decreases. This is the pattern seen in the basic model above, which we call the "beneficial sharing" effect. At higher values of relatedness, it pays Alpha to grant a share of reproduction to Beta because the first few young are cheap for Beta to produce. Again, when $r = 1$ there is no conflict between the breeders, and they agree to produce a total brood size closer to that which is most productive by sharing equally the costs of reproduction.

The two contrasting effects of relatedness on skew are shown clearly in Figure 5 for three levels of costliness of young. The stable level of skew (once again measured by Pamilo and Crozier's index S, defined above) initially rises with relatedness (the incentive effect), but at higher values of relatedness skew declines (the beneficial sharing effect). The point at which Alpha grants reproduction to Beta as a beneficial share rather than as a staying incentive depends on the cost of young. When young are relatively cheap, the incentive effect dominates for all but the highest values of relatedness, and the expected relationship between skew and relatedness is positive for biologically reasonable parameter values. When young are costly, in contrast, Alpha starts to offer a beneficial share at relatively low levels of relatedness, and the correlation between skew and relatedness is for the most part negative.

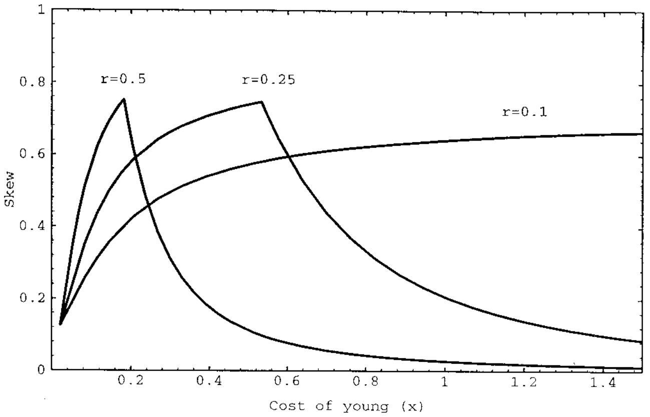

Figure 6
Reproductive skew in the integrated model, measured by Pamilo and Crozier's (1996) index S (defined in text), as a function of x, the relative cost of young. The curves shown are for three values of relatedness. All three curves start to converge as x drops below 0.2. At values of x below the convergence point, Beta does better to disperse and breed independently; $k = 0.2$, $h = 1.5$, $d = 0.6$.

Figure 6 shows the effect of the relative cost of young on the stable level of skew for three values of relatedness. When $r = 0$, it never pays Alpha to offer a beneficial share, so subordinate reproduction always represents an incentive offered by Alpha. At higher levels of relatedness, there is a switching point between incentives and beneficial sharing as costs increase. When costs are very low, incentives predominate. Here an increase in cost is associated with an increase in skew, because the benefit to Beta of dispersing declines relative to that of staying, so Alpha needs to offer less reproduction as an incentive for Beta to stay. As costs rise further, we reach the switching point at which Alpha starts to offer a beneficial share of reproduction to Beta. In this region, skew declines with increasing costs because Alpha benefits more and more from sharing the expense of the brood with Beta.

The three curves in Figure 6 converge as costs become small. The point of convergence is the decision point at which Beta does better to disperse than to stay in the association. Because this point is the same regardless of relatedness, we agree with Reeve and Ratnieks (1993) that relatedness should have no effect on the probability that a subordinate will join an association rather than disperse to breed independently. The model also agrees with that of Reeve and Ratnieks in predicting an overall negative relationship between skew and d, the probability of successful dispersal, though this is not shown in the figures.

DISCUSSION

Models of reproductive skew attempt to identify the factors that determine the division of reproduction in animal societies. Here we have shown that one previously neglected factor, the cost of producing young, can exert an important influence on the stable level of skew within groups. When cost is an accelerating function of the number of young that an individual produces, it will sometimes pay a dominant animal to allow a related subordinate to contribute to the joint brood—not as a staying incentive to keep her in the group, but because additional offspring would be expensive for the dominant to produce but are cheap for the subordinate. Note that costs of rearing that are shared among group members are not relevant to the present argument. Instead, we are concerned with personal costs paid by a parent to produce young—e.g., the costs to avian parents of egg production (which have recently been shown to be comparable with the costs of incubation and provisioning of chicks in some species; Monaghan and Nager, 1997). Incorporating shared costs into the model does not, however, qualitatively alter the results.

Introducing the beneficial sharing effect into existing skew models can alter their predictions quite dramatically. In incentive-based models (Reeve, 1991; Reeve and Ratnieks, 1993), which assume that the dominant has perfect control over subordinate reproduction, related subordinates gain indirect fitness benefits from helping their relatives to breed and so require less in the way of incentives to keep them in the group. In an alternative incomplete control model by Cant (1998), which assumes that dominants cannot prevent subordinates from breeding, related subordinates are selected to add fewer young to the dominant's brood. Both models, therefore, predict a positive relationship between reproductive skew and relatedness. The present analysis, however, reveals that this result depends on the assumptions one makes about the cost of producing young. When costs are relatively low and/or linear the model predicts a positive correlation between skew and relatedness. When costs are high and accelerating the model predicts the opposite relationship because dominants are more likely to offer a beneficial share of reproduction to a related subordinate than to an unrelated one.

Because we have defined cost in terms of opportunities to invest in future young, an accelerating cost function is equivalent to a convex-down relationship between investment in the current brood and adult survivorship, which is a standard assumption in optimal clutch size theory (Charnov and Krebs, 1974; Daan et al., 1990; Kacelnik, 1989). Adding successive young to a single brood is likely to result in ever greater decrements in parental fitness because there is only a finite amount of resources available to invest in both offspring production and survival of the parent itself, and in mammals because increased fetal litter size may also lead to increased energetic costs of locomotion and foraging or increased risk of predation. In contrast, the conditions associated with accelerating costs of young are less likely to apply to continuously breeding species, producing eggs one at a time rather than in litters or clutches, particularly if the mother is freed from the constraints of having to find resources for egg production herself. Such a situation corresponds to that of many social insects, where workers bring resources for egg production to the queen. The current analysis therefore suggests that one should find positive associations between skew and relatedness (as predicted by previous models) in social insects, whereas among communally breeding birds and mammals there is more likely to be no association or even a negative one.

Available data on skew and relatedness in ants and wasps seem to offer preliminary support for the prediction of incentive-based models that high skew will be associated with high relatedness (Bourke, 1997; Bourke and Franks, 1995; Bourke et al., 1997; but see Field et al., 1998). Keller and Reeve (1994; Reeve and Keller, 1995) suggested that there was a similar trend among birds, and in a recent paper they present comparative evidence to this effect (Reeve et al., 1998). However, if we restrict the analysis to skew among females (with which the current model is concerned), we find that there are too few data at present to test this prediction. Of the four species of communally breeding birds in which relatedness and skew between females have been reliably estimated (common moorhen *Gallinula chloropus*: McRae, 1996; pukeko *Porphyrio porphyrio*: Jamieson, 1997; acorn woodpecker *Melanerpes formicivorus*: Koenig et al., 1995; Galapagos mockingbird *Nesomimis galapageonsis*: Curry, 1988; Curry and Grant, 1990), only two (moorhens and pukeko) showed a significant difference between skew in related versus unrelated associations.

In mammals, comparative data offer a similarly inconclusive picture. In naked mole rats (*Heterocephalus glaber*), high skew among females is associated with high relatedness, as predicted by incentive-based skew models. In damaraland mole rats (*Cryptomys damarensis*), however, maximum skew among females is associated with substantially lower levels of intracolony relatedness (Bennett, 1994; O'Riain MJ, personal communication), suggesting that factors other than relatedness (e.g., severe ecological constraints) are likely to have driven the evolution of high skew in the the eusocial Bathyergidae (Faulkes et al., 1997). In lions, all adult females in a pride are close relatives, yet normally all reproduce (Packer et al., 1988, 1991). At an intraspecific level, the strongest support for incentive-based models comes from Creel and Waser's (1991, 1997) studies of dwarf mongooses, among whom female subordinates less closely related to the same-sex dominant are more likely to reproduce. As Clutton-Brock (1998) points out, however, these females also tend to be older and less closely related to male breeders, and both of these factors may provide an alternative explanation for the observed pattern of reproduction (e.g., the dominant may be less easily able to suppress reproduction by older individuals, and subordinate females may avoid mating with closely related males). Further genetic studies of cooperatively breeding vertebrates are required before alternative models based on incentives, beneficial sharing, and limited control can be properly evaluated.

As mentioned above, the present model is relevant only to females and suggests that there is an important distinction to be made between reproductive skew among males and among females. Beneficial sharing is only possible when subordinate reproduction can lead to an increase in the total productivity of the group. Although this may be true among females, it does not apply to males, who usually have no influence over brood size but merely compete for a share of paternity. Consequently, the beneficial sharing approach will be of little use in explaining variation in skew among males, and the incentive-based models of Reeve et al. are likely to be better suited to this task (Cant, 1998; Clutton-Brock, 1998). Thus, among males one would expect only positive associations between skew and relatedness, as has been shown in lions (Packer et al., 1991) and white-fronted bee-eaters (Emlen and Wrege, 1992; reviewed by Reeve et al., 1998). The best way to test this would be to compare skew among males and females in the same society. Social vertebrates in which there are several breeding males and females per group (e.g., banded mongooses, lions, and acorn woodpeckers) may thus prove to be excellent species on which to test the predictions of the current model.

One interesting possibility for future theoretical research suggested by the model is the investigation of multiple breeding events. Because the costs of offspring production are expressed in terms of a reduction in future reproductive success, a fuller analysis would need to consider an individual's opportunties for breeding over 2 or more successive years. This would make explicit the trade-off between greater productivity in one breeding season and the next. Furthermore, the fitness costs of producing a given number of young would then depend on the likely extent of breeding opportunities in the future (because if an individual has little chance to breed in future, there is little to be lost by sacrificing a degree of survival probability in order to raise more offspring during the current breeding attempt).

A futher complication is that production costs suffered by dominants may be reduced by better access to resources, morphological specialization for reproduction (e.g., female naked mole rats; Jarvis et al., 1991), or escape from more costly behavioral roles (e.g., babysitting in suricates; Clutton-Brock et al., 1998). In such cases, the production of young may involve a greater decrement to future fitness for subordinates than for dominants, which will restrict the possibility for beneficial sharing. Assessing the importance of these different factors is difficult because costs are unlikely to be fixed, but they will be influenced by behavioral decisions on the part of group members (e.g., concerning the division of labor involved in brood care). There is thus considerable scope for futher models of beneficial sharing that incorporate individual differences in cost.

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