A model for the evolution of reproductive skew without reproductive suppression

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Abstract. Reproductive skew is a measure of the way breeding is distributed among the members of an animal society or group. Up to now, explanations of patterns of skew have been limited to one particular model, which assumes that a single dominant has full control over the distribution of subordinate reproduction. If this control is incomplete or absent, however, unsanctioned breeding by subordinate females will increase the total number of young produced. Here I present a new model for the evolution of skew that considers the effect of brood size on the inclusive fitness of dominants and subordinates. By augmenting brood size, a subordinate female reduces the per capita fitness of a dominant's offspring, so the net benefits of producing young are lower for related subordinates. I consider the stable level of skew when both dominant and subordinate attempt to maximize their inclusive fitness under two conditions: (1) when the dominant is unable to anticipate that a subordinate will add to her brood; and (2) the dominant does anticipate subordinate reproduction and can respond by adjusting her own brood size. In the first case, the model predicts that reproductive skew will increase with relatedness between breeders, because related subordinates are selected to add fewer young to the dominant's brood. In the second case, the dominant's optimal response to the presence of a second breeder exaggerates the relationship between relatedness and skew: dominants should produce more young when breeding with related compared with unrelated subordinates.

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Attempts to find unifying principles in diverse cooperative breeding systems have recently centred on 'reproductive skew', which is a measure of the way in which direct reproduction is shared among members of a social unit (Reeve & Keller 1995). At two ends of a continuum are high skew societies characterized by the monopolization of breeding by a single individual, and low skew societies in which breeding is distributed equitably among group members. Recent models of the evolution of reproductive skew suggest that variation in the costs and benefits of subordinate breeding to the dominant determines the level of reproductive suppression imposed by the dominant. Vehrencamp (1983a, b) provided an illuminating model using this approach, and the idea has been extended by Reeve (1991), Reeve & Ratnieks (1993) and Reeve & Keller (1995). These

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models reveal that (in conjunction with ecological factors) kin selection may play an important role in the evolution of skew: a dominant associating with a related subordinate can monopolize direct reproduction by exploiting the subordinate's kin-selected incentive to stay as a helper; an unrelated subordinate lacks this indirect benefit of staying and the dominant must grant her a share of direct reproduction to maintain the association. Thus one of the main predictions of the model is that reproductive skew will be high where relatedness between group members is high. Empirical support for this prediction is presented by Keller & Reeve (1994) and Reeve & Keller (1995).

Critically, these models assume that the dominant has full control over the distribution of a fixed amount of parentage: the extra direct fitness that is assumed to arise from an association is shared out by the dominant on a zero-sum basis in the manner that maximizes her own inclusive fitness. If the dominant does not have full control over the level of subordinate reproduction,

however, breeding by subordinate females will result in a larger overall brood size, and the total amount of direct fitness available to be shared will then depend on how offspring fitness varies with brood size. In singular breeding species (i.e. those in which one female in the breeding group produces young) per capita fitness of young is expected to be a negative function of brood size, so that the total number of viable surviving young declines as brood size becomes large (Lack 1947; Lessels 1991). It is reasonable to suppose that this negative relationship will also apply for plural breeders, in which two or more females in a social unit breed together (Brown 1987), whenever their young compete for a share of limited space or resources. Thus by increasing brood size, a subordinate female will reduce the per capita fitness of a dominant's offspring, and if this female is related to the dominant, producing young will entail indirect fitness costs.

This paper is concerned with the evolution of skew in mating systems where dominants do not have control over subordinate reproduction and where helping is absent. I present a simple two-female kin selection model based on the effect of breeding by a subordinate female on the fitness of a combined brood. The model addresses two questions concerning the influence of relatedness between breeders on the level of reproductive skew: (1) how does relatedness influence the optimum number of young for a subordinate to produce; and (2) how many offspring should a dominant produce when a second female will also contribute to the brood? I examine the stable level of skew when both parties attempt to maximize their inclusive fitness by adjusting their own production of young.

THE MODEL

Consider the decision of a single female, called beta, of whether to breed with another female called alpha. Alpha and beta are used to signify a basic asymmetry in the game between the breeders: alpha 'moves' first, producing her own optimum number of young, and beta then chooses her best option given alpha's decision.

For simplicity assume a linear decrease of individual offspring fitness with brood size, so that:

$$\lambda(c) = 1 - kc$$

where $\lambda(c)$ is the probability of an individual offspring surviving to maturity in a brood of size c and the constant k is a measure of the sensitivity of offspring fitness to crowding (Mangel & Clark 1988). Thus the total fitness of a brood of size c is given by:

$$W(c) = c\lambda(c) \tag{1}$$

To begin with, alpha is assumed to produce the brood size that maximizes $f(n)$, the direct benefits minus the direct costs of producing young, given that the total offspring fitness function is $W(c)$ regardless of whether one or two females breed. In the basic model, alpha's brood size is the same whether or not she is joined by another breeding female; later I consider the case when alpha can respond to the presence of another breeder by adjusting her own brood size.

Let $\mu(n)$ be the cost of producing n young (assumed to be linear). Thus

$$f(n) = W(n) - \mu(n)$$

or

$$f(n) = n(1 - kn) - \mu n \tag{2}$$

Maximizing equation (2), alpha's optimum brood size n^* is given by:

$$n^* = \frac{1 - \mu}{2k} \tag{3}$$

Next I consider how many offspring beta should produce given that alpha produces clutch size n^*. The rationale is that beta will be selected to produce the brood size that maximizes her inclusive fitness payoff $P(i) + r\Delta F(i)$, where r is the coefficient of relatedness between alpha and beta, $P(i)$ is beta's direct fitness when producing i young, and $\Delta F(i)$ is the change in alpha's direct fitness when beta produces i young, compared with when beta does not breed (Hamilton 1964; Grafen 1991).

First, I develop an expression for alpha's direct fitness as a function of combined brood size. Beta can add m offspring to alpha's brood to raise the combined brood size to $c = n^* + m$. Let the proportion of young in the brood that are alpha's be denoted by p, and beta's by q, so that $p = n^*/(n^* + m)$, and $q = m/(n^* + m)$. If one assumes that total combined brood fitness $W(c)$ is shared

according to the relative contributions of the two breeders, the direct fitness payoff for alpha (F_α) arising from the brood is given by:

$$F_\alpha = pW(c) - \mu n^*$$

To calculate beta's inclusive fitness payoff, I include the negative effect she has on alpha's direct fitness by deciding to breed, devalued by r, her relatedness to alpha. Her payoff through breeding is therefore

$$IF_\beta = qW(c) - \mu m + \\ r[(pW(c) - \mu n^*) - (W(n^*) - \mu n^*)] \quad (4)$$

Using $n\lambda(c)$ and $m\lambda(c)$ for $pW(c)$ and $qW(c)$ respectively, I maximize this function and solve for $m^*(n^*)$, beta's optimum allocation to the combined brood, that is, the number of offspring that maximizes her payoff through breeding, given that alpha produces brood size n^*. The solution is given by:

$$m^*(n^*) = \frac{1 - \mu}{2k} - \frac{n^*(1 + r)}{2} \quad (5)$$

Figure 1 shows the results of the model for three values of relatedness. Both beta's maximum payoff, $IF_{\beta max}$, and her optimal combined brood size c^* (where $c^* = n^* + m^*(n^*)$) decrease with increasing relatedness to alpha. The effect is due to the increasing weight of the negative indirect component of equation (4) as relatedness increases.

Beta's proportion of young in the combined brood (q) equals $m^*(n^*)/(n^* + m^*(n^*))$. Substituting the expressions for n^* and $m^*(n^*)$ (equations 3 and 5) gives, after simplification,

$$q = \frac{1 - r}{3 - r} \quad (6)$$

The shape of this function is shown as curve A in Fig. 2. Since the proportions p and q are equivalent to the degree of reproductive skew between alpha and beta, a main prediction of the model is that skew between breeders increases as relatedness increases.
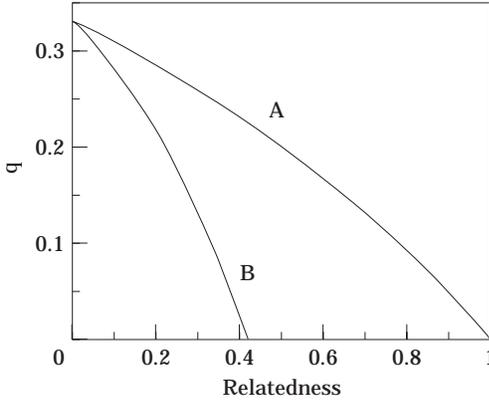
The Extended Model

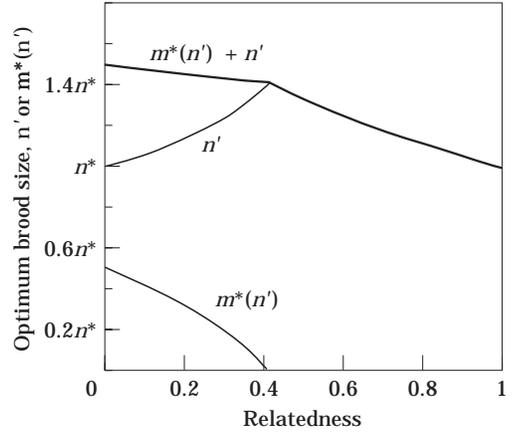I now ask whether alpha will be selected to alter her brood size from n^* if another female in the
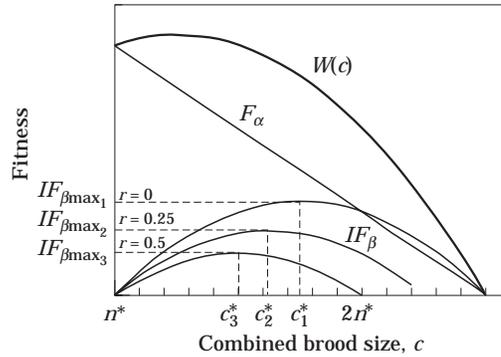
Figure 1. Inclusive fitness payoff to a subordinate breeder (IF_β), and direct fitness of a dominant (F_α) as a function of brood size. A dominant breeding solitarily produces brood size n^*. $W(c)$ is total fitness return on a brood of size c, and is given by $W(c) = c(1 - kc)$, where the constant k measures the rate of decline of individual offspring fitness with brood size. Each young costs μ fitness units to produce. (In the example shown $\mu = 0.2$, $k = 0.4$, $n^* = 1$.) The optimal combined brood size for a subordinate female for three values of relatedness to the dominant ($r_1 = 0$, $r_2 = 0.25$, $r_3 = 0.5$) is given by c_i^*. As relatedness increases, the maximum inclusive fitness payoff a subordinate female can obtain through breeding ($IF_{\beta max_i}$) decreases, as does the optimum number of young she should add to the brood (shown as a reduction in her optimal combined brood size c_i^*).

group is liable to produce young. When considering alternative strategies available to alpha, it becomes necessary to find an expression for alpha's inclusive fitness that will include a component for the effect of her chosen brood size on beta's direct fitness. As in the basic model, alpha's brood size when the sole breeding female is n^*. Alpha anticipates that beta will breed and can respond by adjusting her own production of young. I seek alpha's stable optimum brood size: that which maximizes her inclusive fitness given that the number of young she produces determines beta's optimum brood size.

I express alpha's inclusive fitness payoff as a function of n, given that for each n, beta produces her own optimum number of young $m^*(n)$. To simplify things, I include beta's whole direct fitness in the expression for alpha's inclusive fitness payoff rather than just the change in beta's direct fitness that results from alpha's decision. This yields an identical result when solving for optimal brood size.

Figure 2. The proportion of direct reproduction obtained by beta (q) as a function of relatedness in the basic model (curve A), and the extended model (curve B). In the basic model, alpha produces brood size n^* and beta contributes the number of young that maximizes her own inclusive fitness. Since the proportion of reproduction obtained by beta is inversely equivalent to the level of reproductive skew, skew increases with relatedness. In the extended model alpha anticipates breeding by beta and adjusts her own brood size to maximize her inclusive fitness. q declines with relatedness more sharply than in the basic model, until alpha monopolizes breeding completely when $r \geq \sqrt{2} - 1$. (Parameters: $\mu = 0.2$, $k = 0.4$.)

Let $IF_\alpha(n)$ equal the inclusive fitness payoff of brood size n so that:

$IF_\alpha(n) = [\text{direct benefit of } n$
$\quad - [\text{direct cost of } n]$
$\quad + r[\text{beta's direct fitness}$
$\quad\quad \text{when alpha produces } n]$

More formally,

$$IF_\alpha(n) = pW(c^*(n)) - \mu n + r[qW(c^*(n)) - \mu(m^*(n))] \quad (7)$$

where $c^*(n) = m^*(n) + n$. Equation (7) can be rewritten as:

$$IF_\alpha(n) = n\lambda(n + m^*(n)) - \mu n + r[m^*(n)\lambda(n + m^*(n)) - \mu m^*(n)]$$

Beta's optimum allocation for each n, $m^*(n)$, is given by equation (5). Substituting into the above expression, I obtain a function that is differentiable with respect to n. Solving for n', the

Figure 3. Total combined brood size and optimum brood size of alpha (n') and beta ($m^*(n')$), against relatedness, r, in the extended model. Alpha's brood size when the sole breeding female is n^*. When alpha anticipates that beta will also breed, the optimum number of young for her to produce rises with relatedness, and beta's optimum declines, until n' reaches a maximum of $\sqrt{2}n^*$ at $r = \sqrt{2} - 1$. At this point beta's optimum allocation is zero. At higher levels of relatedness, beta's optimum brood size remains zero while alpha's optimum size declines, reaching n^* at $r = 1$. Total combined brood size declines from $1.5n^*$ at $r = 0$ to n^* at $r = 1$. (Parameters: $\mu = 0.2$, $k = 0.4$.)

brood size that maximizes alpha's inclusive fitness payoff, I obtain:

$$n' = \frac{1 - \mu}{k(2 - r(1 + r))} \quad (8)$$

for $r < \sqrt{2} - 1$. For $r > \sqrt{2} - 1$. $m^*(n') = 0$, and alpha's optimum brood size is

$$n' = \frac{1 - \mu}{k(1 + r)} \quad (9)$$

Figure 3 shows the optimum individual brood size for alpha (calculated from equations 8 and 9) and beta (from equation 5) as a function of relatedness. Also shown is the total size of the combined brood. For $r = 0$, $n' = n^*$, that is, alpha's optimum brood size when $r = 0$ is the same as that which she produces when breeding alone. As relatedness increases, alpha's inclusive fitness is maximized by producing successively larger broods, and the optimum number of young for beta to produce declines. Alpha's optimal brood

size reaches a maximum of $n' = \sqrt{2}n^*$, and beta's optimum allocation reaches zero when $r = \sqrt{2} - 1$. At this point alpha's enlarged brood size makes breeding unprofitable for beta. At higher levels of relatedness, the number of extra young that alpha must produce to keep beta's optimum allocation at zero declines, until her brood size returns to n^* at $r = 1$.

Beta's proportion of reproduction (derived from equations 5 and 8) up to the point where her optimum allocation is zero (i.e. $r < \sqrt{2} - 1$) is given by

$$q = \frac{1 - r(2 + r)}{3 - r(2 + r)} \qquad (10)$$

The proportion of the brood contributed by beta (from equation 10) as a function of relatedness in the extended model is shown as curve B in Fig. 2. When alpha anticipates reproduction by a second breeder and can alter her own brood size, beta's proportion of reproduction declines much more rapidly as relatedness increases, until her contribution reaches zero (i.e. breeding becomes non-profitable) for $r \geq \sqrt{2} - 1$.

DISCUSSION

Discussions of reproductive skew are usually made with reference to dominant and subordinate animals, where dominant status implies some form of active control over the reproductive output of subordinates (Vehrencamp 1983a, b). There are often obvious differences in reproductive output between social group members, however, without it being clear whether this is due to socially imposed suppression or individual reproductive restraint (Creel & MacDonald 1995). In this paper I have assumed that neither player has the power to permit or prohibit the reproduction of the other directly, but there is none the less a basic asymmetry between alpha and beta in the level of control each animal has over her own ideal production of young: alpha first optimizes her brood size given that she will be joined by a second breeder of known relatedness, and this decision places constraints on the options available to the beta female. One might picture the role of beta as corresponding with that of a newly mature subordinate in a social group in which alpha is an established dominant breeder. The

important point is that beta's decision is made in the certainty that alpha will breed, and moreover will produce her optimum brood size. For convenience, and with the asymmetry of their constraints in mind, I equate the roles of alpha and beta with that of dominant and subordinate in this discussion.

Reproductive skew is predicted to be higher in groups composed of relatives, for three reasons. First, a related subordinate is selected to add fewer young to the dominant's brood because the indirect costs of reducing the fitness of the dominant's offspring weigh more heavily as relatedness increases. Consequently, the model predicts that the individual reproductive success of the dominant will be greater when breeders are related. Second, if brood size is flexible, a dominant is selected to increase her own brood size when breeding with a relative, but not when the second breeding female is unrelated. A dominant produces successively larger broods with increasing relatedness to the subordinate, since by doing so she raises the indirect fitness cost of any young the subordinate may contribute. At high levels of relatedness the costs to the beta female of contributing further to a much enlarged combined brood may increase to the extent that they outweigh the direct fitness benefits and breeding becomes non-profitable. Somewhat paradoxically then, the model suggests that under some circumstances a subordinate may inflict a cost on the dominant by her presence at the nest (by causing the alpha female to produce a larger-than-optimal brood size), and yet produce no young at all. Both parties would benefit if the subordinate gave some sort of signal that she would not breed, and hence there was no need for the dominant to adjust her brood size. The stability of such a signal might be addressed using signalling theory (e.g. Grafen 1990).

Finally, there is the subordinate's decision of whether to breed, disperse or stay as a non-breeder. The maximum fitness obtainable through breeding for a given brood fitness function $W(c)$ is lower for related females, so they are more likely to favour alternative strategies such as dispersal or staying as a non-breeder over breeding. Thus, in common with optimal skew models (Vehrencamp 1983a, b; Reeve & Ratnieks 1993; Reeve & Keller 1995), ecological constraints on independent breeding will influence the observed level of skew. Unlike previous treatments, however, the model

makes no assumption about whether associations are more productive than single breeders, and so can account for the evolution of skew in the absence of a helping effect. This may be particularly important for social vertebrates, where it is not always clear whether helpers actually help. For example, 17 out of 33 studies of cooperatively breeding birds reported no significant effect of helpers on breeding success (from reviews of Brown 1987 and Emlen 1991). Nevertheless, if we do assume that the presence of a subordinate benefits the reproductive success of the dominant, the conclusions of the model are reinforced: a related subordinate's kin-selected incentive to stay as a non-breeder increases the net benefit of the non-breeding option relative to that of breeding, at least if helping and breeding are to some extent mutually exclusive.

The model assumes a negative relationship between offspring fitness and brood size. The slope of this function will depend on the extent to which additional parental investment by a second female can offset the costs of increased within-brood competition. In the model presented here, however, the parameter describing this slope, k, cancels out of the expression for the proportion of the brood contributed by beta, q. This is an artefact of assuming that both offspring fitness and the cost of producing young are linear functions of brood size. Nevertheless, the basic model appears to be quite robust with regard to these assumptions. If one assumes the offspring fitness function to be convex downwards (which might be more realistic), k does not cancel out of the expression for q, but its effect is weak and the main results of the model are unchanged. Similarly, it makes little difference to the relationship between relatedness and beta's proportion of the brood if one assumes that the cost of producing young is an exponential rather than linear function of brood size (unpublished simulations). Although I have not analysed the extended model in this way, one might expect that here an exponential cost function would lead to lower skew between breeders of given relatedness: the cost of increases in brood size much past n^* will be prohibitive for alpha, so that beta may take advantage of the relatively low cost of her own young and increase her proportional contribution to the brood.

Available empirical data on the relationship between relatedness and skew in insects, birds and mammals lend support to both this and optimal skew models (reviewed by Keller & Reeve, 1994; Reeve & Keller 1995). Little information is available about the cost to a dominant's fitness of additions to the brood by subordinates (but see McRae 1996). In Arabian babblers, *Turdoides squamiceps*, and pukeko, *Porphyrio porphyrio*, total combined brood size is larger when two females contribute to a nest, but individual reproductive success of joint-nesting females is lower than that of females who breed on their own (Craig 1980; Zahavi 1990). Koenig et al. (1983) reported that groups of acorn woodpeckers, *Melanerpes formicivorus*, in which two females contributed to the clutch produced fewer fledglings than groups in which only one female laid. Effects such as these, however, may arise because lower quality females are more likely to form associations. To remove such confounding factors, experimental manipulation of clutch size, carried out a number of times in singular breeding birds (Lessels 1991), could be used in plural breeding species to assess the function relating the fitness of dominants' and subordinates' offspring to clutch size.

The model is explicitly relevant only to females, and differs in important respects when applied to male breeders. Breeding by a subordinate male results in a loss of a share of paternity for the dominant, but the total fitness being shared between males is not reduced. The net benefit of breeding to subordinate males is an increasing linear function of their level of paternity, the slope of which decreases with increasing relatedness between subordinate and dominant. By contrast, as they add to a dominant's brood, subordinate females suffer increasing indirect fitness costs and receive decreasing direct fitness benefits (because of crowding). For subordinate females there is an intermediate optimum level of direct reproduction, but subordinate males should attempt to gain the greatest possible share of paternity. Thus skew among males will always be determined by the degree of control one individual has over another's reproduction. I started by assuming that dominants have no control whatsoever over subordinate reproduction to contrast with previous models, but as the situation for males makes clear, such an assumption is probably equally unrealistic. Both male and female dominants will usually have some means of undermining the breeding attempts of subordinates, through monopolization of resources, harassment, or

infanticide (Emlen & Wrege 1992; Creel & MacDonald 1995; Koenig et al. 1995). The model also implicitly assumes that the fitness of offspring does not depend on the identity of their parent, but it may often be that dominants produce more viable young. However, though these effects will serve to reduce the net benefit of breeding for subordinates, the disparity between related and unrelated subordinates will remain, both in their optimal brood size and in the maximum fitness they can realize through breeding, unless unrelated subordinates are singled out for greater harassment.

ACKNOWLEDGMENTS

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