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Female Control of the Distribution of Paternity in Cooperative Breeders

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ABSTRACT: Models of reproductive skew have shed light on why animal societies vary in the partitioning of reproduction among group members. However, their application to cooperative vertebrate societies remains controversial. A particular problem is that previous models assume that skew in paternity is determined by interactions among males and males only. This conflicts with observations from many species that indicate that females exert control over the distribution of paternity. Here we address this shortfall in the current theory by developing two models to explore the expected patterns of skew in three member groups in which a female controls the allocation of paternity among two males. The first "staying incentive" model extends previous "transactional" (or "concession") models to examine the conditions where females will be willing to share reproduction among a dominant and a subordinate male to retain the subordinate in the group. The second "work incentive" model explores patterns of skew where females allocate paternity in order to maximize the amount of care their offspring receive. The models make contrasting predictions about the nature of male-female conflict over reproduction and also about the relationships between skew and relatedness, ecological constraints, the relative quality of the subordinate male, and the relative cost of care for the two males. These divergent predictions provide a schema by which the evolutionary causes of variation in skew among males can be evaluated.

Keywords: reproductive skew, paternity, cooperative breeding, helping.

The last decade has seen a surge of interest in the theory of reproductive skew, which aims to explain variation across animal societies in the distribution of reproduction among group members. Pioneering skew models were based on the idea that dominant individuals exert full control over reproduction but may sometimes gain by allowing subordinates to breed as an incentive for them to remain in the group and help with offspring care (Vehrencamp 1983; Reeve 1991; Reeve and Ratnieks 1993). These transactional ("concessions") models have been extended to incorporate the possibility of multimember groups (Johnstone et al. 1999), subordinate inheritance (Kokko and Johnstone 1999; Ragsdale 1999), competition between multiple dominants (Reeve 1998), and dominant manipulation (Crespi and Ragsdale 2000). Comparative evidence from social insects has provided support for these models (Reeve and Keller 2001), but their applicability to cooperatively breeding vertebrates has been the subject of some debate (Cant 1998, 2000; Clutton-Brock 1998*a*, 1998*b*; Emlen et al. 1998; Reeve et al. 1998; Cant and Johnstone 1999; Johnstone 2000; Koenig and Haydock 2000; Magrath and Heinsohn 2000; Clutton-Brock et al. 2001; Cant et al. 2001). In particular, vertebrate biologists have called into question the assumption that dominant individuals have full control over reproduction, spurring the development of "incomplete control" models of skew (Cant 1998; Reeve et al. 1998; Johnstone and Cant 1999; Johnstone 2000).

The development of alternative skew models has forced a reappraisal of the way in which the models can be tested empirically. Nevertheless, theoretical gaps remain. Perhaps the most important of these for the study of skew in vertebrates is that all of the models described above analyze conflict between individuals of the same sex, ignoring the fact that most cooperatively breeding vertebrates live in mixed-sex groups (Koenig and Haydock 2000; Legge and Cockburn 2000; Magrath and Heinsohn 2000). This means that applications of the original skew models to explain skew among males (whether based on concessions or incomplete control) must assume that the division of paternity is decided by interactions among males and males only. This assumption is at odds with observations in many species, suggesting that females exert control over the distribution of paternity (Davies 1992; Eberhard 1998; Whittingham and Dunn 1998; Cant 2000).

Here we address this gap in the theory by developing

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two models to examine expected patterns of skew in a multimale group in which the female has control over the division of paternity. The first extends the classical skew framework of Reeve (1991) and Reeve and Ratnieks (1993); the second is based on models of female control of paternity to maximize overall paternal care developed by Harada and Iwasa (1996) and Houston et al. (1997). As we show, the models make divergent predictions, providing an opportunity to distinguish them empirically.

The Model

Consider a female who can breed in a pair with an adult male, whom we call "alpha," or in a trio with an additional male named "beta." In the first model, which we call the "staying incentive model," we assume that the beta male will leave the group unless he achieves a minimum paternity and solve for this minimum paternity (a "staying incentive") as a function of the value of parental care, beta's expected reproductive output if he disperses, and the relatedness between males.

Alpha is dominant to beta in the sense that he can potentially evict beta from the group, whereas beta is unable to evict alpha. The productivity of the three-member group with beta present is denoted k, relative to the productivity of the female–alpha male pair, which we set equal to 1. For this model, we assume that productivity k is independent of the way the female distributes paternity between the two males; what matters is whether the beta male remains in the group or not. This assumption will hold where helping effort is not related to paternity, or where males exactly compensate for changes in each other's helping effort, leaving total investment more or less constant (see appendix). We compare the predictions of this model with those of previous, single-sex skew models.

In the second model, the "work incentive model," we allow for the possibility that the productivity k depends on the apportionment of paternity among the males. In particular, we incorporate the assumption of recent models that a male's parental investment is an increasing function of its paternity such that the female can maximize the total productivity by having the males share paternity. The predictions of this model are compared with those of the staying incentive model.

Staying Incentive Model

We assume that alpha and beta vary in genetic quality, such that offspring fathered by alpha have expected reproductive success proportional to q_α and those fathered by beta have expected reproductive success proportional to q_β (see also Shellman-Reeve and Reeve 2000). The ratio of these qualities, q_β/q_α, is denoted by y and is referred to as the "relative quality of beta." Here we assume that beta is of lower genetic quality than alpha (i.e., $y < 1$), which establishes a preference in the female for one male over the other. The female and alpha would do best if alpha sired all of the young (such young are assumed to have the highest genetic quality), but then both might run the risk of losing the beta's parental care. Ecological constraints on independent breeding are incorporated in the parameter x, which gives the probability of a male breeding successfully outside the group. If beta disperses, his expected direct fitness is $q_\beta x$. We assume that the female is unrelated to either of the males but that the males are symmetrically related to each other by coefficient r.

Given the above assumptions, beta does best to stay in the group rather than disperse if the following inequality is satisfied:

$$pq_\beta k + r(1 - p)q_\alpha k > q_\beta x + rq_\alpha,$$

where p is the fraction of reproduction obtained by beta. Substituting $y = q_\beta/q_\alpha$, converting the inequality into an equality, and solving for p yields beta's staying incentive (Reeve and Ratnieks 1993), that is, the minimum fraction of reproduction required by beta to make staying in the group worthwhile. The solution is

$$p_{\min} = \frac{xy + r(1 - k)}{k(y - r)}. \qquad (1)$$

For $x < r(k - 1)/y$, $p_{\min} \leq 0$, that is, beta will stay in the group without any share of reproduction.

Note that the sign of the denominator of $p_{\min}$ depends on the relative magnitude of r and y. As will become evident below, the model makes different predictions depending on whether r is greater or less than y. In most biologically plausible situations, however, it is probably safe to assume that $r < y$; the only exceptions will occur where males are closely related (e.g., brothers), and yet the quality of the alpha male is more than twice that of the beta male. Theoretical studies suggest that genetic quality among males is unlikely to vary by more than 5%–10% (Austin 1995); moreover, as relatedness increases, one would expect the difference in genetic quality to decrease. Accordingly, we hereafter consider only the case of the model where $r < y$, while noting the theoretical possibility of alternative predictions given $r > y$.

The alpha male and the female may disagree over the offering of the staying incentive. From the perspective of the alpha male, the staying incentive $p_{\min}$ should only be offered to beta where the following inequality holds:

$$(1 - p_{\min})q_{\alpha}k + rp_{\min}q_{\beta}k > q_{\alpha} + rq_{\beta}x,$$

which yields the condition $x < k - 1$ (see also Reeve and Ratnieks 1993).

From the female's perspective, however, the staying incentive $p_{\min}$ should be offered when this results in greater productivity than she could expect from breeding in a pair with alpha. More formally, she should offer the staying incentive provided the following inequality is satisfied:

$$(1 - p_{\min})q_{\alpha}k + p_{\min}q_{\beta}k > q_{\alpha},$$

which after substituting (1) above yields the condition

$$x < \frac{(1 - k)(r - 1)}{1 - y}. \tag{2}$$

However, the range over which the female can offer $p_{\min}$ may be further constrained because the alpha male may gain from evicting beta if beta receives too large a share of reproduction. The alpha male does best to tolerate beta rather than evict him if

$$(1 - p_{\min})q_{\alpha}k + rp_{\min}q_{\beta}k > (1 - e)q_{\alpha} + rxq_{\beta},$$

where e is the additive cost to alpha of evicting beta (see also Johnstone and Cant 1999). Again, after substitution of (2) above, this yields the following condition for which the female can safely offer $p_{\min}$ to beta without triggering eviction by alpha. The condition is

$$x < \frac{y(k - 1)(r^2 - 1) + e(r - y)}{y(r^2 - 1)}. \tag{3}$$

The zone of conflict between the alpha male and the female over the offering of the staying incentive can therefore be summarized as $k - 1 < x < x_{\max}$, where

$$x_{\max} = \min\left\{\frac{(1 - k)(r - 1)}{1 - y}, \frac{y(k - 1)(r^2 - 1) + e(r - y)}{y(r^2 - 1)}\right\}.$$

These zones of agreement and conflict between the female and the alpha male are illustrated in figure 1. Where $x < r(k - 1)/y$, the subordinate will stay with no reproduction. In the region $r(k - 1)/y < x < k - 1$, the female and the alpha male both agree that beta should be offered the staying incentive $p_{\min}$. However, as x rises above $k - 1$, alpha does best to withdraw the staying incentive and let beta disperse. The female, by contrast, is selected to continue offering $p_{\min}$ until $x > x_{\max}$ at which point either alpha evicts beta or else the female no longer profits from sharing paternity with beta and withdraws the staying incentive. In either case, the three member group becomes unstable.

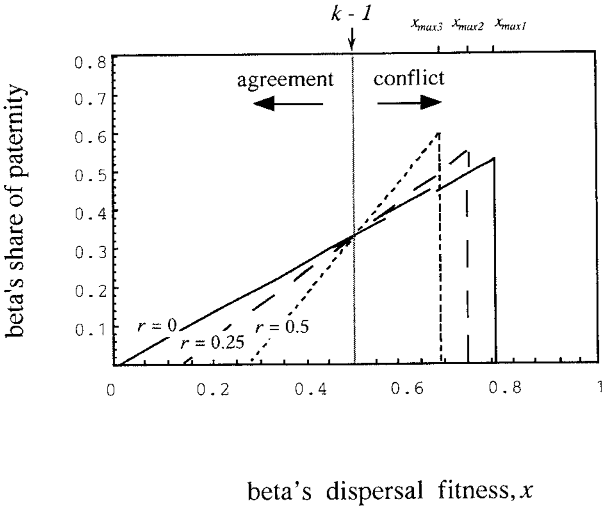


Figure 1: Beta's share of paternity as a function of dispersal fitness in the staying incentive model, for three values of relatedness, $r = 0$, $r = 0.25$, and $r = 0.5$. In the zone of agreement, where $x < k - 1$, both the female and the alpha male favor the offering of the staying incentive to the beta male. As x rises above $k - 1$, the group enters the zone of conflict in which the female, but not the alpha male, favors the offering of the staying incentive to beta. The female will continue to offer the staying incentive up to $x = x_{\max i}$ (in the figure, $x_{\max 1}$ for $r = 0$, $x_{\max 2}$ for $r = 0.25$, $x_{\max 3}$ for $r = 0.5$; other parameters: $k = 1.5$, $e = 0.3$, and $y = 0.9$).

Predictions concerning Skew in Paternity

Beta's share of reproduction is given by $p_{\min}$. We can derive simple predictions concerning the degree of reproductive skew in the system by simple inspection of (1) or by examining the sign of the partial derivative of $p_{\min}$ with respect to r, k, x, and so forth. These partial derivatives are given in table 1.

The partial derivative of $p_{\min}$ with respect to relatedness (see table 1) is negative for $x < k - 1$ and positive otherwise. Thus, where $x < k - 1$, that is, in the zone of agreement, beta's fraction of reproduction decreases as relatedness increases (fig. 2*a*), in agreement with the prediction of concession models (Vehrencamp 1983; Reeve and Ratnieks 1993). However, in the zone of conflict between the alpha male and the female, $k - 1 < x < x_{\max}$, beta's share of reproduction increases with relatedness between the two males (fig. 2*b*). This occurs because in the zone of conflict between the alpha male and the female the beta is inflicting a cost on the alpha by remaining in the group and must therefore receive a larger direct fitness share from the female to counter this indirect fitness cost. Where females control the allocation of paternity and where they are in clear conflict with dominant males over the distribution of paternity, the model predicts that skew in paternity will decrease as relatedness between males increases.

The partial derivative of p_{min} with respect to k is negative given our assumption that $r < y$. Thus, the model predicts that skew in paternity will be higher the greater the productivity boost associated with retaining the beta male, in agreement with concession models of skew (Vehrencamp 1983; Reeve and Ratnieks 1993). This is because a beta male who confers a large productivity benefit will need a relatively smaller fraction of that productivity in order to balance the payoffs of staying versus dispersing.

The relationship between beta's share of reproduction and x is revealed by simple inspection of expression (1): clearly, p_{min} increases with x (see also table 1). Skew in paternity is therefore expected to decrease as ecological constraints on male dispersal become weaker, in agreement with concession models. As x increases, a larger share of paternity is required to balance the payoff the beta male could expect by dispersing.

Finally, the partial derivative of p_{min} with respect to y is positive for $x < k - 1$ and negative for $x > k - 1$. This means that in the zone of agreement skew in paternity will decrease as the relative quality of the beta male increases. In the zone of conflict between the alpha male and the female, skew in paternity is expected to increase with the quality of the beta male. This is because in the zone of conflict beta inflicts a cost on the alpha male by remaining in the group, and the beta must be compensated for this indirect fitness cost by a slightly bigger share of direct fitness. The lower the relative genetic quality of beta, the greater the fraction of reproduction required to compensate beta for the cost he inflicts on alpha.

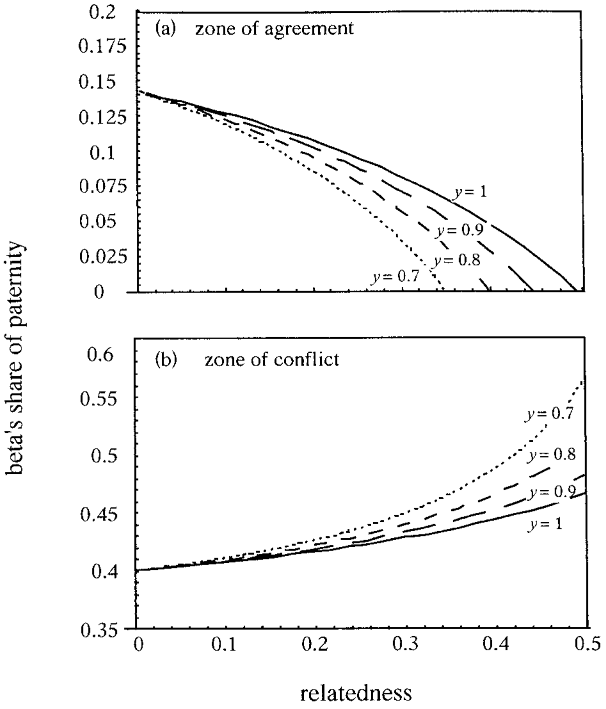


Figure 2: The effect of relatedness on beta's share of paternity in the staying incentive model in (*a*) the zone of agreement ($x < k - 1$) and (*b*) the zone of conflict ($k - 1 < x < x_{\mathrm{max}}$) for four values of y, the relative quality of beta. Relatedness has opposite effects on skew in the zone of agreement versus the zone of male-female conflict. Other parameters: (*a*) $x = 0.2$, $k = 1.4$, and $e = 0.3$; (*b*) $x = 0.6$, $k = 1.4$, and $e = 0.3$.

Work Incentive Model

The model presented in the previous section demonstrates that females may be selected to share reproduction among males even if the overall productivity of a stable three member group, k, does not depend on the way in which paternity is distributed among the two males. In many cooperatively breeding birds and mammals, however, females are thought to encourage matings with more than one male so as to maximize the level of paternal investment directed toward their offspring (Davies 1992; Westneat and Sherman 1993; Houston et al. 1997; Wright 1998). In this

Table 1: Effect of changes in staying incentive model parameters on the share of reproduction allocated to the beta male

	Relatedness r	Productivity k	Dispersal fitness x	Beta's genetic quality y
Partial derivative of p_{min}	$\frac{\partial p_{\mathrm{min}}}{\partial r} = \frac{y(1-k+x)}{k(r-y)^2}$	$\frac{\partial p_{\mathrm{min}}}{\partial k} = \frac{r+xy}{k^2(r-y)}$	$\frac{\partial p_{\mathrm{min}}}{\partial x} = \frac{y}{k(y-r)}$	$\frac{\partial p_{\mathrm{min}}}{\partial y} = \frac{r(k-1-x)}{k(r-y)^2}$
Positive or negative	− ($x < k - 1$) + ($x > k - 1$)	−	+	+ ($x < k - 1$) − ($x > k - 1$)

Note: A positive partial derivative indicates that increasing the parameter in question leads to an increase in beta's share of paternity; a negative partial derivative indicates the opposite.

section, we develop an alternative model, the work incentive model, which assumes that variation in the level of skew among males influences how hard males work but does not influence the decisions of the males as to whether to stay or disperse. In other words, productivity k is a function of the fraction of paternity p allocated to beta.

We arrive at this function $k(p)$ by examining how each male should invest in the brood according to his share of paternity rather than by assuming some relationship between productivity and the distribution of paternity. Our approach is based on that of Houston and Davies (1985), who analyze the responses of two individuals to changes in each other's level of parental investment. Evolutionarily stable levels of investment are found by determining the best response of each player to the effort of the other and solving for the Nash equilibrium at which neither player can do better by shifting to another level of effort (Cant and Field 2001; but see McNamara et al. 1999 for a critique of this approach). The method was recently employed by Harada and Iwasa (1996) to consider how a female should distribute paternity so as to maximize the level of parental investment by two unrelated males. Here we extend these models to consider trios in which the two males may be related by coefficient r and may vary in relative genetic quality y, as in the staying incentive model.

We assume that alpha and beta can invest in the female's offspring at a level h_α and h_β ($0 \leq h \leq 1$). (For simplicity, we do not consider here the female's evolutionarily stable levels of investment.) Let the productivity of the current brood G increase linearly with total investment such that $G(h_{\text{tot}}) = g(h_\alpha + h_\beta)$, where g is a constant that determines the productivity benefit of a given level of help by the alpha and beta male (similar results are obtained if one assumes that productivity increases with individual investment at a decelerating rate; see also Harada and Iwasa 1996). Following previous models, we assume that residual reproductive value w declines with investment at an accelerating rate (Houston and Davies 1985; Houston et al. 1997). In particular, we assume that alpha and beta's reproductive values are given by

$$w_\alpha = 1 - h_\alpha^{m_\alpha}, \tag{4}$$

$$w_\beta = y(1 - h_\beta^{m_\beta}), \tag{5}$$

where m_α and m_β are constants describing the rate at which the reproductive value of alpha and beta, respectively, fall off with increasing individual investment (m_α and m_β are assumed >1). Larger values of m imply that investment in young is initially relatively cheap, with reproductive value falling off only at high levels of investment. We define the ratio $d = m_\alpha/m_\beta$ as the relative cost of care for beta. Where $d > 1$, care is more costly for beta than alpha; the opposite holds for $d < 1$. In a recent article, Houston et al. (1997) show that the precise distribution of paternity that maximizes the level of parental investment is sensitive to changes in the shape of the functions relating investment to reproductive value (4) and (5) above. However, the qualitative results of our model hold for a range of convex-down fitness functions (including those of Houston et al. 1997) for which female fitness is maximized at some intermediate value of p (as opposed to female fitness being maximized at $p = 1$ or 0).

The inclusive fitnesses of alpha and beta are written as follows:

$$W_\alpha = (1 - p)q_\alpha G(h_{\text{tot}}) + w_\alpha + r[pq_\beta G(h_{\text{tot}}) + w_\beta], \tag{6}$$

$$W_\beta = pq_\beta G(h_{\text{tot}}) + w_\beta + r[(1 - p)q_\alpha G(h_{\text{tot}}) + w_\alpha]. \tag{7}$$

The optimum levels of effort for the males, which we denote h_α^* and h_β^*, are found by solving the simultaneous equations $\partial W_\alpha/\partial h_\alpha = 0$ and $\partial W_\beta/\partial h_\beta = 0$ for h_α and h_β. This yields the solutions

$$h_\alpha^* = \left[\frac{m_\alpha}{g(1 - p + pry)}\right]^{1/(1-m_\alpha)},$$

$$h_\beta^* = \left[\frac{m_\beta y}{g(r - pr + py)}\right]^{1/(1-m_\beta)},$$

and we can now derive the function relating productivity k to beta's share of paternity p as $k(p) = g(h_\alpha^* + h_\beta^*)$.

The female's reproductive success (or direct fitness) is given by

$$W_{\text{f}} = (1 - p)k(p) + pyk(p),$$

and the optimum distribution of paternity from the female's perspective, p_{fem} is found by differentiating W_{f} with respect to p, setting equal to zero and solving for p.

Predictions concerning Skew in Paternity

The equation $\partial W_{\text{f}}/\partial p = 0$ does not yield a simple analytical solution, so we solve the model numerically and present representative results in figures 3 and 4. The main results are also given in figure 5.

Figure 3 shows beta's share of paternity as a function of relatedness between the two males for four values of y, the relative genetic quality of beta. Where $y < 1$, beta's share of paternity decreases with relatedness. The reason for this is that both males increase investment with increasing relatedness, but the rate at which alpha's investment increases with relatedness is greater than that of beta.

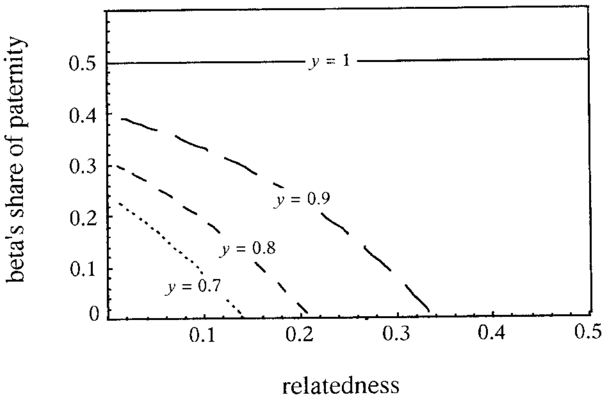


Figure 3: The effect of relatedness on beta's share of paternity in the work incentive model for four values of y, the relative quality of beta. Note that when there is no difference in quality between alpha and beta, females should split paternity equally among the two males, irrespective of relatedness. Other parameters: $g = 2$, $m_\alpha = 3$, $m_\beta = 3$.

Thus, the female can allocate a smaller amount of paternity to beta (who is, after all, genetically inferior to alpha) while still maximizing the total investment she receives. Where there is no difference in genetic quality between the two males ($y = 1$), the optimum allocation between the males is constant (50 : 50 in our model; but see Houston et al. 1997 for other possibilities), regardless of relatedness. This prediction would also hold for cases where females are unable to distinguish genetic quality among the two males.

Figure 4 shows how beta's share of paternity changes with the relative cost of his care, relative to that of the alpha male. Beta's share of paternity increases with the relative cost of his care. This is because, as care becomes increasingly costly for the beta male, his optimum level of effort for a given level of paternity decreases. The female can induce the beta male to work harder by offering him a greater share of paternity.

Finally, we test whether there will be conflict over the allocation of paternity by comparing the optimum distribution of paternity from the female's perspective with that from the perspective of the alpha male. Alpha's preferred distribution, p_{alpha}, is found by substituting our expression for $k(p)$ in place of $G(h_{\text{tot}})$ in (6), differentiating with respect for p and solving for $\partial W_\alpha / \partial p = 0$. The alpha male will be in conflict with the female where $p_{\text{fem}} > p_{\text{alpha}}$. As before, numerical methods must be employed to find p_{alpha}. Our numerical results indicate that the inequality $p_{\text{fem}} > p_{\text{alpha}}$ holds for all biologically plausible combinations of parameter values. We conclude, therefore, that there is always conflict between the female and the alpha male over the distribution of paternity in the work incentive model.

Discussion

Despite a large literature on the ways in which females may influence the distribution of paternity among males in an attempt to maximize their own reproductive success (reviewed by Eberhard 1998), models of reproductive skew in cooperatively breeding groups have until now been restricted to games between individuals of the same sex. We have presented two models to explore the expected patterns of skew in cases where females control the distribution of paternity. The predictions of the two models are summarized in figure 5.

Figure 5 lays out the type of information necessary to test which model, the staying incentive or work incentive model, best accounts for the variation in skew among males seen in nature. A first step is to examine the patterns of conflict among the sexes over the sharing of paternity. In a few species (e.g., golden lion tamarins: Baker et al. 1993; pukeko: Jamieson et al. 1994; Galápagos hawk: Faaborg et al. 1995; Tasmanian native hen: Goldizen et al. 2000), there is little or no overt mating conflict between males or between males and females. This is difficult to explain via the work incentive model, in which females always prefer a more even distribution of paternity than dominant males. Rather, the lack of conflict between alpha males and females in these species is consistent with the staying incentive model, which predicts a zone of agreement in which both the female and the dominant male benefit from the allocation of a share of paternity to beta in order to retain him in the group. Note, however, that the staying incentive model does allow for conflict between

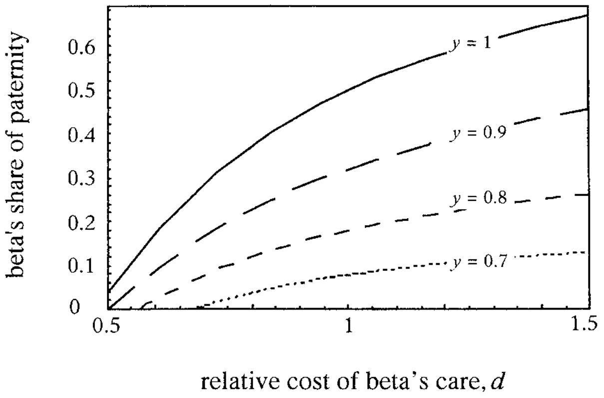


Figure 4: The effect of the relative costliness of beta's care on his share of paternity in the work incentive model for four values of y, the relative quality of beta. Other parameters: $g = 2$, $m_\alpha = 4$, $r = 0.1$.

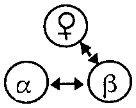
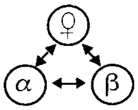
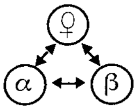
Model	patterns of conflict	increasing relatedness	increasing productivity boost of beta's presence (or of male care)	increasing ecological constraints	increasing genetic quality of beta	increasing cost of beta's care
staying incentive ($x < k - 1$)		↑	↑	↓	↓	N/A
staying incentive ($x > k - 1$)		↓	↑	↓	↑	N/A
work incentive		↑ ($y < 1$)	↓ 0 ↑	0	↓	↓

Figure 5: A comparison of the effect of various parameters in the staying incentive model and the work incentive model on the level of reproductive skew among males. Upward arrows indicate an increase in skew; downward arrows indicate a decrease in skew; zeros indicate no effect. Diagrams in the "patterns of conflict" column indicate expected direction of conflict (overt or otherwise) between members of the trio.

the female and the subordinate male, and between the two males, since the beta male will be selected to try to claim more than his minimum staying incentive, whereas the alpha male and the female will both be selected to prevent him from doing so. Where females and dominant males agree over the distribution of paternity, the predictions of previous classical skew models should hold. Indeed, patterns of skew among male pukeko are consistent with these predictions (Jamieson 1997).

Examples of such harmonious allocation of paternity are rare, however. In most multimale societies of cooperatively breeding vertebrates, dominant males go to considerable lengths to guard females against the mating attempts of other group members (e.g., birds: see reviews in Stacey and Koenig 1991; also Davies et al. 1996; Legge and Cockburn 2000; mammals: Rood 1986; Packer et al. 1991; Cant 2000). Where there is mate guarding or other behavioral conflict between females and dominant males, the staying incentive and work incentive models make contrasting predictions regarding the relationship between skew and relatedness; ecological constraints; the subordinate's genetic quality; and the relative cost of care for the subordinate male. In conjunction with information on male-female conflict, future tests could usefully focus on the effect of these parameters in order to distinguish the two models.

Some existing data from cooperatively breeding species in which there is male-female conflict weigh against the staying incentive model. Experiments have been performed in a number of cooperatively breeding species in which the perceived share of reproduction by subordinate males is reduced by preventing them from mating with females during their fertile period (reviewed by Wright 1998). These experiments were aimed at testing whether males' effort varies with their certainty of paternity. In each case, male removals led to a reduction in the subordinate male's level of parental care, which is consistent with both models (see appendix). However, the manipulation of skew did not lead to the dissolution of the group, as one might expect under the staying incentive model.

Both our models assume that females have full control over the distribution of paternity, but the fact that males go to such effort to guard females suggests that they have at least some chance of constraining the paternity share obtained by the subordinate male. The consequences of alpha males exerting partial control over the distribution of paternity are radically different for the two models. In the work incentive model, dominant males may be able to claim a larger share of paternity than is optimum from the female perspective without compromising the stability of the group: the only consequence would be an increase in skew and a reduction in total productivity of the brood. In the zone of conflict of the staying incentive model, by contrast, the alpha male need only reduce beta's share by the smallest amount in order to induce him to disperse. This means that where the alpha male has partial control over the allocation of paternity, groups in the zone of conflict of the staying incentive model are expected to be unstable, ruling out the predictions in the second row of figure 5.

The proliferation of skew models over the past few years has led to the complaint that almost any pattern of reproduction might be explained by one model or another. On the contrary, we agree with Hilborn and Mangel (1997) that the formulation of alternative models usually represents a progression in the understanding of a natural system. Since all models are inconsistent with the data to some degree, a model cannot be rejected until there is available an alternative, more consistent model (see also Lakatos 1978). In our view, the main problem with research in this area is that most empirical studies have focused on testing model predictions without checking whether their assumptions are likely to hold in the breeding system under consideration. The two models presented here confirm the importance of evaluating which party, male or female, controls paternity in multimale vertebrate societies before attempting to test the models' predictions. For example, one could test whether females have full control of paternity by removing alpha males for short periods during the fertile period. If females fully control the distribution of paternity, one would expect the removal of alpha males to have little consistent effect on their share of paternity. By contrast, if alpha males normally exercise control over paternity, their removal should lead to a reduction in their share of paternity. Tests of this nature will allow alternative models to be rejected on the basis of their assumptions, simplifying and bringing much-needed rigor to the study of reproductive skew in nature.

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APPENDIX

Total Productivity and the Distribution of Paternity

Imagine a species in which males can estimate their level of paternity and adjust their paternal care accordingly. Let male investment increase linearly with share of paternity. The slope of the curves of paternity against investment are α for alpha and β for beta. Thus, the total productivity in a stable three member group is

$$k(p) = 1 + \alpha(1 - p) + \beta p,$$

which after rearranging becomes

$$k(p) = 1 + \alpha + p(\alpha - \beta).$$

Our assumption that k is constant implies $(\alpha - \beta) = 0$, that is, that alpha and beta use the same rule-matching paternity to investment in the region where they receive shares $(1 - p)$ and p, respectively.

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