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Reproductive skew and the threat of eviction: a new perspective

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Most recent models of the partitioning of reproduction attempt to explain patterns of skew on the assumption that dominant individuals have complete control over breeding opportunities within the group, but may nevertheless concede a share of direct reproduction to subordinates as an incentive to remain peacefully in the association. Although these models may be applicable to some animal societies, we argue that they fail to provide a comprehensive theory of skew. Instead, we suggest that subordinates may often be able to claim unsanctioned reproduction for themselves, but will be forced to exercise a degree of reproductive restraint lest they incite ejection by the dominant. Reproductive skew, in other words, may reflect the threat of ejection (inducing subordinate restraint) rather than the threat of subordinate departure (inducing reproductive concessions by dominants). We present a simple evolutionarily stable strategy model of reproductive skew under these circumstances, which demonstrates that a shift in emphasis from reproductive concessions by dominants to reproductive restraint on the part of subordinates, radically alters the predictions of skew models. High group productivity, high relatedness and (when group members are related) strong ecological constraints are all expected to lead to reduced skew (the opposite conclusions to those of previous, concession-based analyses). The reason is that these factors reduce the benefits (or increase the costs) of ejection to the dominant, who therefore does best to tolerate more subordinate reproduction.

Keywords: cooperative breeding; reproductive suppression; sociality; aggression; game theory

1. INTRODUCTION

The distribution of reproduction varies greatly among animal societies (Keller & Reeve 1994). In some groups, which are said to exhibit high reproductive skew, one or a few individuals are able to monopolize breeding. In others, which are said to exhibit low reproductive skew, breeding is more equitably distributed among all group members. What factors are responsible for such variation?

Most recent models of the partitioning of reproduction attempt to explain patterns of skew on the assumption that dominant individuals have complete control over breeding within the group, but may nevertheless concede a share of direct reproduction to subordinates as an incentive to remain peacefully in the group (Vehrencamp 1979, 1983*a*,*b*; Reeve & Ratnieks 1993; Reeve 1998; Johnstone *et al.* 1999). 'Concession' models of this kind predict that skew will be high when ecological constraints on dispersal are tight, group members are closely related and/or association yields considerable productivity benefits (because under these circumstances, subordinates require less of a reproductive incentive to remain in the association).

Although there is evidence to support the above predictions in a few species (e.g. Creel & Waser 1991; Reeve 1991; Bourke & Heinze 1994; Jamieson 1997; but see Creel & Waser 1997; Field *et al.* 1998, for contrary examples), it is far from obvious that dominants do always have full control over breeding. Subordinates may often be able to claim an unsanctioned share of reproduction, simply because dominants are unable to prevent them from doing so (see Cant 1998; Clutton-Brock 1998; Reeve *et al.* 1998). The presence of the subordinate could thus be detrimental rather than beneficial to the dominant.

An observation that supports this alternative perspective is that in many species, dominant group members are known to forcibly evict or exclude subordinates from the group, while the subordinates themselves are clearly reluctant to leave. This occurs among birds (e.g. Tasmanian native hens, Maynard Smith & Ridpath 1972; pied kingfishers, Reyer 1986; Arabian babblers, Zahavi 1991; dunnocks, Davies 1992; oropendolas, Webster 1994; splendid fairy wrens, Mulder 1995), mammals (e.g. grey langurs, Sugiyama 1967; vervet monkeys, Henzi & Lucas 1980; spotted hyenas, Holekamp *et al.* 1993; house mice, Gerlach 1996; black tufted-ear marmosets, Schaffner & French 1997; suricates, Clutton-Brock *et al.* 1998; banded mongooses, M. A. Cant, unpublished data; Damaraland mole-rats, R. Cooney, unpublished data) and fishes (e.g. the cooperatively breeding cichlids, *Neolamprologus brichardi*, Taborsky 1985; *N. pulcher*, Balshine-Earn *et al.* 1998).

Forcible eviction (or exclusion) is hard to accommodate within the framework of concession models. If the dominant has full control over breeding within the group, as these models assume, then the presence of subordinates cannot threaten its reproductive monopoly, but will simply boost productivity. As a result, forcible ejection

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can only reduce the dominant's fitness. In addition, because subordinates cannot hope to acquire unsanctioned reproduction, they do best to depart voluntarily whenever the dominant is unwilling to yield sufficient staying incentives. From the perspective of concession models, in other words, forcible eviction appears to be unnecessary as well as unprofitable.

Instead, we argue that subordinates often can claim unsanctioned reproduction for themselves. The dominant may thus have reason to evict other group members, because they threaten its breeding monopoly. Subordinates, in turn, will be forced to exercise a degree of reproductive restraint lest they incite such a response. Reproductive skew, in other words, may reflect the threat of ejection (inducing subordinate restraint), rather than the threat of subordinate departure (inducing reproductive concessions by dominants).

Here, we develop a simple evolutionarily stable strategy model of skew in which subordinates can claim unsanctioned reproduction, but must exercise restraint in order to avoid being evicted. To facilitate comparison with previous analyses, we base our model on the 'transactional' framework of Reeve & Ratnieks (1993; see also Reeve & Keller 1997). Our emphasis, however, is on the reproduction that subordinates must forego in order to prevent eviction, rather than the reproduction that dominants must forego in order to prevent subordinate departure.

2. REPRODUCTIVE SKEW, EVICTION AND SUBORDINATE RESTRAINT

We focus on an association of two individuals, an established dominant and a subordinate. Following Reeve & Ratnieks (1993), we will use k to denote the total productivity of such an association, relative to that of a lone established breeder. However, whereas Reeve & Ratnieks (1993) assume that $k > 1$, we impose no such restriction. Values of $k < 1$ (which we permit, but do not require) simply imply that total productivity is reduced when a subordinate joins the group. This might be due to greater competition for limiting resources in the breeding territory, overproduction of young, or time and effort devoted to reproductive suppression, competition and interference (see Koenig *et al.* 1983, 1995; Vehrencamp *et al.* 1986; Ratnieks & Visscher 1989; Creel *et al.* 1992; Bourke 1994; Cant 1998; Johnstone & Cant 1999).

We assume that the subordinate can potentially claim at least some share of direct reproduction for itself, despite any attempts by its associate to prevent this. The upper limit on the proportion it claims is ultimately set, not by any direct interference on the part of the dominant, but by the threat of ejection from the group. In other words, the subordinate must exercise a degree of reproductive restraint to ensure that the dominant has insufficient incentive to evict it from the association.

If the dominant does choose to eject the subordinate, it (the dominant) incurs an additive direct fitness cost e, reflecting the time and energy involved, and the possible risk of injury if the subordinate resists (note that in addition to this direct cost, we also take account of possible indirect costs, if ejection leads to a reduction in survival or reproductive success of a related subordinate). Following Reeve & Ratnieks (1993), the direct fitness gained by a subordinate who is ejected (or who departs voluntarily) will be denoted x. While Reeve & Ratnieks assume that x is always positive, however, we will allow negative values. $x < 0$ (which we permit but do not require) simply implies that the lifetime direct fitness of a subordinate who leaves the group is lower than that of one who remains in the association without obtaining any share of direct reproduction in the current breeding attempt. Such negative values are likely if group membership brings benefits in the form of improved survival prospects (Pulliam & Caraco 1984) or a chance to accede to dominance status following the death of the current dominant (Emlen 1991; Lucas *et al.* 1997; Kokko & Johnstone 1999; Ragsdale 1999); under these circumstances, departure may entail a direct fitness cost, rather than a benefit.

Assuming that subordinate breeding is limited only by the threat of eviction, the share of direct reproduction that the subordinate obtains, denoted p, will be the largest value it can claim without triggering ejection, i.e. the largest value for which the dominant still does best to tolerate rather than to eject the subordinate. Writing r for the coefficient of relatedness between the two individuals, the dominant does best to tolerate the subordinate whenever

$$k((1-p)+rp) > 1-e+rx, \tag{1}$$

(the left-hand side in the above inequality represents the inclusive fitness consequence of tolerance from the dominant's point of view; the right-hand term, the inclusive fitness consequence of ejection). Solving for p and converting the inequality into an equality, we obtain the maximum share of reproduction that the subordinate can safely claim, denoted p^*,

$$p^* = \frac{e+(k-1)-rx}{k(1-r)}. \tag{2}$$

Note that unless

$$k > 1+rx-e, \tag{3}$$

p^* is negative, implying that the subordinate cannot afford to claim any direct reproduction for itself. Under these circumstances, a stable association is not possible, because the dominant always stands to gain from ejection (even when the subordinate does not reproduce).

Having calculated p^*, the maximum share of reproduction that the subordinate can afford to claim, it remains to be determined whether this is enough to make it worthwhile staying in the group. The subordinate does best to remain in the association whenever

$$k(p+r(1-p)) > x+r, \tag{4}$$

(the left-hand side in the above inequality represents the inclusive fitness consequence of staying, the right-hand term, the inclusive fitness consequence of departure; note that the dominant does not suffer a direct cost of ejection if the subordinate leaves voluntarily).

Substituting the value of p^* given by equation (2) for p in inequality (4), we find (after some manipulation) that the association is stable only if

$$x < (k-1)+\frac{e}{1-r}. \tag{5}$$

Provided that inequality (5) is satisfied, the share of reproduction that the subordinate can claim (without rendering ejection worthwhile for the dominant) is large enough that she does best to remain in the group. Together, inequalities (3) and (5) yield sufficient conditions for a stable group.

3. RESULTS

Inspection of equation (2) immediately reveals that p^*, the maximum share of direct reproduction that the subordinate can afford to claim, increases with e (the direct fitness cost of ejection to the dominant). The explanation for this is simple. When ejection entails substantial direct fitness costs, it is not worthwhile unless the subordinate threatens to claim a large share of reproduction. In other words, the greater the direct cost of ejection to the dominant, the greater the amount of subordinate reproduction it does best to tolerate.

From equation (2), it is also clear that p^* decreases with x (the direct fitness consequences of dispersal for the subordinate), provided that the two group members are related. In other words, the model suggests that subordinates will receive a smaller share of reproduction when ecological constraints are weak, the opposite prediction to that of concession-based analyses. The reason for this is that a subordinate will suffer less from ejection under these circumstances, reducing the indirect fitness cost of eviction from the (related) dominant's point of view. Reduced costs for the dominant, in turn, mean that it will tolerate less subordinate reproduction.

Although the effects of k (group productivity) and r (relatedness) are less immediately obvious from equation (2), increases in both typically lead to increases in p^*. In other words, subordinates should be able to acquire a larger share of reproduction when group productivity and relatedness are high, once again the opposite predictions to those of concession-based analyses. The reason is that high productivity and high relatedness both lead to high costs of ejection for the dominant; the former, because the productivity benefits of association are lost if the subordinate is evicted, the latter, because the indirect costs of eviction to the dominant are increased if it is closely related to the subordinate whom it ejects. Both factors thus favour increased tolerance on the part of the dominant, allowing subordinates to claim a greater share of reproduction. The only exception to this pattern occurs when ecological constraints are so weak that the likely breeding success of a subordinate who disperses exceeds the productivity benefits of association. Under these circumstances, the dominant is actually more likely to eject a closely related subordinate (since it gains greater indirect fitness benefits from the breeding success of a closer relative); consequently, the maximum share of reproduction that the subordinate can claim decreases with relatedness under these circumstances.

Turning to the condition for group stability given in inequality (5), when $e = 0$ (i.e. there are no direct costs of ejection), this matches the condition derived by Reeve & Ratnieks (1993) in their concession-based analysis. Under these circumstances, both models predict that associations are more likely to prove stable when group productivity is high and ecological constraints are strong (while relatedness has no influence on stability). In our model, however, the range of conditions over which the association will prove stable also increases with e, and this effect is more marked the more closely related the subordinate is to the dominant. Ejection costs promote stability because they increase the likelihood that the subordinate can claim a sufficient share of reproduction to make staying pay, while still being tolerated by the dominant. The reason this effect is stronger when the two group members are more closely related is that the dominant then has less to gain by preventing subordinate reproduction, so that the direct costs of ejection become relatively more significant.

4. DISCUSSION

The above analysis reveals that a switch in emphasis from reproductive concessions given by dominants to reproductive restraint on the part of subordinates, radically alters the predictions of skew models. The threat of ejection from the group is more telling when ecological constraints are weaker, group members are less closely related and the productivity benefits of association are lower. Consequently, these are the conditions under which our model predicts that subordinates must exercise more restraint, and that skew will therefore be high. At the same time, these are the very conditions under which concession models predict that larger staying incentives will be required, and that skew will consequently be lower. How are we to reconcile these contrasting conclusions?

Our model sets an upper limit on the share of direct reproduction that subordinates can acquire. Even if the dominant has severely limited control over the allocation of reproduction within the group, the threat of ejection ensures that subordinates can never obtain a share larger than our p^* (defined in equation (2)) in a stable association (unless they are able to conceal their reproductive activity from the dominant, a possibility that is not dealt with in the present model). By contrast, concession models set a lower limit on the share of direct reproduction that subordinates will acquire. Even if the dominant has complete control over the allocation of reproduction within the group (as existing concession models in fact assume), it must yield a share at least as great as the 'staying incentive' of Reeve & Ratnieks (1993) to avert the threat of subordinate departure (see Reeve & Keller 1997).

We obtain opposite predictions to concession-based analyses because the same factors that render association profitable from the subordinate's point of view, and thus reduce the staying incentive it requires, also render association profitable from the dominant's point of view, and thus increase the level of subordinate reproduction it is prepared to tolerate. When group members are closely related, group productivity is high and/or ecological constraints are tight, the threat of departure and the threat of ejection are both weak; consequently, the minimum share of reproduction that dominants must offer is small, but the maximum share that subordinates can claim is large. Conversely, when group members are only distantly related, group productivity is low and/or ecological constraints are weak, both threats become more pressing; as a result, the minimum share that dominants must offer is larger, while the maximum share that subordinates can claim is smaller.

In practice, the relative importance of the contrasting predictions made by our present model and by concession-based analyses depends on the extent to which dominant individuals control reproduction within the group. When control is complete, subordinates will only receive that share of reproduction that dominants must offer them as an incentive to remain peacefully (i.e. the lower limit calculated in concession models). By contrast, the weaker the control exerted by dominants (and the more pressing the threat of eviction), the more likely it is that subordinates will be able to claim the maximum share of reproduction that dominants will tolerate without ejecting them (i.e. the upper limit calculated in our model). The fact that the upper and lower limits on reproduction are most divergent when relatedness and group productivity are high and ecological constraints are tight, suggests that variation in the extent of dominant control over reproduction will have the most influence on patterns of skew under these circumstances.

Our contention (and the motivation for developing the present model) is that in many animal societies, dominants may often lack full control over subordinate breeding. Instead, we suggest that the threat of ejection may often represent the dominant's chief weapon in the conflict over reproduction. The notion of subordinate restraint may thus be of more use than that of reproductive concessions in explaining patterns of skew among such species.

Dominance displays (ranging from the production of pheromones to overt acts of aggression), from this perspective, may be viewed as signals of the dominant's ability to evict a recalcitrant subordinate from the group (see Keller & Nonacs (1993) for a related suggestion). The implication is that intense display behaviour induces reproductive restraint on the part of subordinates, because it indicates that the dominant can easily bear the costs of ejection, and so is less likely to tolerate a subordinate who claims a large share of reproduction (in terms of the present model, intense display indicates a low value of e). The costs involved in such a display will serve to maintain its honesty, since a stronger dominant who can more easily eject a recalcitrant subordinate is also likely to find expensive display behaviour less of a burden (Johnstone 1997).

Data regarding levels of skew in different vertebrate populations and species are currently too few to assess the relative significance of reproductive concessions and of subordinate restraint on a broad scale. Predictions regarding the level of skew (in relation to parameters such as group productivity or relatedness) are not, however, the only way assess the applicability of different theories of skew. We have already alluded to the widely reported observations of forcible ejection of subordinates, which suggest that the assumptions of concession models are inappropriate in at least some cases. A second factor which argues for the importance of eviction is the possibility of status inheritance. Among longer-lived organisms (such as many vertebrates), subordinates may well stand to gain by remaining in the group even without a share of direct reproduction, because they can ultimately hope to accede to breeding status following the death of the current dominant (for discussion see Emlen 1991; Lucas *et al.* 1997; Kokko & Johnstone 1999; Ragsdale 1999). Moreover, these future benefits (combined with any survival advantage of group membership) are likely to induce subordinates to continue joining the group until it exceeds the most productive size (see Sibly 1983; Giraldeau 1988; Higashi & Yamamura 1993). Far from offering incentives to retain subordinates who would otherwise be unwilling to remain, the dominant may thus stand to gain by forcibly ejecting individuals whose presence is detrimental (from its own point of view).

To conclude, recent claims that concession-based models may provide a comprehensive theory of skew (e.g. Keller & Reeve 1994; Reeve *et al.* 1998) are, in our opinion, misguided. Such a theory cannot be reduced to a single type of model, based on a single set of assumptions. Different assumptions are required in different biological contexts (see also Cant & Johnstone 1999). At the very least, skew theory must incorporate both of the concepts outlined above—not only the notion of reproductive concessions offered by dominants, but also that of reproductive restraint exercised by subordinates in response to the threat of eviction.

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