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Reproductive skew theory extended: The effect of resource inheritance on social organization

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ABSTRACT

In social species, resource inheritance is a common and widespread phenomenon. Potential inheritance payoffs may influence an animal's decision of whether to attempt individual reproduction, or to associate with a resource owner as a hopeful reproductive. These alternative reproductive decisions form the crux of reproductive skew theory (RST), which predicts if groups will form and, if so, the extent that reproduction is shared, given the ecological constraints, cooperative benefits, relatedness and relative fighting abilities of group members. I extend RST to include resource inheritance, a form of future direct benefits. Resource inheritance allows relaxation of one restrictive assumption of other RST models, the cooperative benefits assumption. Furthermore, with resource inheritance, stable associations will form over a greater range of conditions than that found in previous models, thus reducing the need for a 'social contract'. Inclusion of resource inheritance generates predictions that are relevant to many social systems, including (under some conditions) parental facilitation, 'lazy workers', helping for 'payment', and complete skew when relatedness is zero or cooperative benefits are absent. The model has general applications because the resource inheritance parameter represents any form of future benefits arising from social associations.

Keywords: future fitness, queue, reproductive skew, resource inheritance, social organization.

INTRODUCTION

Life-history theory predicts a trade-off between current and future reproductive effort (Stearns, 1992). Empirical deviations from Lack's clutch size clearly illuminated the need to consider future effects on present performance (e.g. Charnov and Skinner, 1984). When animals are faced with alternative decisions, they are expected to choose the pathway that yields the greatest lifetime reproduction, if acting adaptively. Dispersal decisions and timing of reproduction are traits that are best understood as life-history decisions, and resource inheritance probably affects both of these decision types. Resource inheritance can occur when the longevity of limited and valuable resources required for reproduction exceed individual lifetimes. For example, resource inheritance can affect dispersal decisions when high-quality territories or oviposition sites remain relatively constant over several generations, thus selecting for natal philopatry (Waser, 1988). In saturated habitats, delayed

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reproduction may be favoured until resources become available, by the death of the owner. An alternative to delayed reproduction is dispersal and settlement into gaps. Herein lies a life-history trade-off: organisms may either attempt relatively risky early reproduction or opt to delay reproduction by queuing for resources. It is precisely these alternative reproductive pathways – that is, whether to associate with a resource owner or to reproduce independently – that form the crux of reproductive skew theory (Vehrencamp, 1983a,b; Reeve and Ratnieks, 1993; Keller and Reeve, 1994).

Reproductive skew theory (RST), a theory of social organization, identifies four factors which predict whether social groups will form and, if so, the degree to which reproduction is shared within groups. The suggested key factors are: (1) ecological constraints, (2) co-operative benefits, (3) relatedness and (4) relative fighting abilities (Reeve and Ratnieks, 1993). However, because present reproductive decisions may be influenced by future expectations, a comprehensive theory of social organization ought to include both present and future aspects. Accordingly, Brown (1980) categorized inclusive fitness into four components: present direct and indirect benefits, and future direct and indirect benefits.

Resource inheritance is a common class of future direct benefits, and its role in social organization has been acknowledged in numerous taxa, including (but not limited to) mongooses, jackals, red foxes, hoatzins, woodpeckers, woodhoopoes, babblers, jays, sphecid, polistine and stenogastrine wasps, bumblebees, halictid bees, allodapine bees, termites and myrmicine ants (see Myles, 1988; Emlen, 1991). However, the evolution of a queuing strategy not only demands a decision to delay reproductive attempts by the queuing individual, but also demands acceptance, or tolerance, by the current resource owner, assuming queuing requires physical proximity. If queuing does occur, then some form of social organization will result. The conceptual framework of RST is conducive to considering whether an individual should queue and, if so, whether a resource owner should allow the presence of the queuing individual.

Currently, RST is receiving considerable empirical and theoretical attention (e.g. Creel and Waser, 1991; Reeve and Nonacs, 1992; Reeve and Ratnieks, 1993; Bourke and Heinze, 1994; Keane *et al.*, 1994; Keller and Reeve, 1994; Bourke and Franks, 1995; Emlen, 1995, 1999; Heinze, 1995; Reeve and Keller, 1995; Sherman *et al.*, 1995; Evans, 1996; McRae, 1996; Pamilo, 1996; Bourke *et al.*, 1997; Crespi and Choe, 1997; Jamieson, 1997; Scott, 1997; Whittingham *et al.*, 1997; Cant, 1998; Clutton-Brock, 1998; Field *et al.*, 1998; Reeve, 1998; Reeve *et al.*, 1998). One of RST's attractive features is its generality; its application spans across taxonomic boundaries and addresses many different forms of social structure, from communal societies to eusociality (Sherman *et al.*, 1995). With the advent of DNA techniques, relatedness values can be accurately obtained (e.g. Evans, 1993), while RST's other variables can be measured as well. Furthermore, RST generates falsifiable predictions (Crespi and Choe, 1997) and thus is amenable to empirical tests. However, RST presently does not consider the life-history trade-off of current versus future reproductive efforts, or include the body of literature with respect to the importance of resource inheritance on social organization (e.g. Wiley and Rabenold, 1984; Stacey and Ligon, 1987; Myles, 1988). Given that organisms have been moulded by natural selection to maximize lifetime reproduction (direct or indirect), an understanding of their behaviour demands a consideration of the *lifetime* implications of each alternative decision (Stearns, 1992). Here I extend RST to include resource inheritance, a general class of future direct reproduction.

MODEL

To assess the influence of resource inheritance on social organization, I extend Reeve and Ratnieks' (1993) two-breeder reproductive skew model, following their methodology. Their model assumes a rank asymmetry between two individuals, a dominant and a subordinate. The cause of asymmetry between the two potential breeders is not specified, but can be viewed as a difference arising from the dominant's ownership of a resource necessary for reproduction, such as a nest or a territory. The dominant is assumed to control the subordinate's reproduction and the reproductive output of a group is assumed to exceed that of an already established solitary individual. Again, the cause of the relative increase in reproductive output, or cooperative benefits, is not specified, but it is assumed to be a fixed value (Reeve and Ratnieks, 1993; Vehrencamp, 1983a,b). But because this cooperative benefits assumption is often violated in nature, I explore the consequences when cooperative benefits are absent. I later explore the conditions under which subordinates should help, assuming that the cooperative benefits parameter is a consequence of subordinate help and thus under subordinate control.

The foundation of RST (Reeve and Ratnieks, 1993) is the premise that a subordinate has two primary options: (1) to join a dominant or (2) to leave and attempt independent reproduction. This decision is mediated by the subordinate's expected reproductive success if it leaves, and by its expected inclusive fitness benefits if it joins. Because RST assumes that the dominant controls the subordinate's reproduction, if it is beneficial for a dominant to associate with a subordinate, it will offer the subordinate some direct reproduction, as a 'staying incentive'. It is assumed that the subordinate and the dominant know the relative payoffs to these alternative strategies and can act adaptively. Furthermore, a subordinate faces another decision – whether to cooperate peacefully or to fight in an attempt to kill the dominant to monopolize all reproduction. Thus here, the dominant is assumed to assess the fighting ability of the subordinate (i.e. the probability it will win the fight) and, if necessary, offer the subordinate a 'peace incentive' (i.e. direct reproduction). Therefore, RST predicts how reproduction can be distributed among group members, when associations are favoured, such that neither the subordinate nor the dominant can increase their fitness given the decisions each is expected to take. Throughout this section, I refer to direct reproduction in the context of reproduction achieved by a subordinate during an association with a dominant. The term 'resource inheritance' refers to future direct reproduction achieved by the subordinate, which is external to the association between a particular subordinate and dominant.

The variables of RST (Reeve and Ratnieks, 1993) are as follows, plus the additional parameter of resource inheritance:

- x = *ecological constraints*, or the expected reproductive success of a subordinate attempting independent reproduction. This variable includes the cost of dispersal, the probability of reproductive establishment, and the expected number of offspring relative to an already established solitary individual (standardized at 1).
- r = *relatedness*, or the ratio of the coefficient of relatedness of an individual to its own offspring and its relatedness to the other group member's offspring. Since this ratio can be asymmetrical between group members, Reeve and Keller (1995) differentiate between the relatedness of a dominant to the subordinate's offspring (r_{ds}) and vice-versa (r_{sd}). For simplicity, this differential relatedness notation is not included in the model here but can easily be added for completeness.

- k = *cooperative benefits*, or the average total reproductive output of a group of two. Note that the reproductive output of an already established solitary breeder is standardized at 1.
- f = *subordinate fighting ability*, or the probability that a subordinate will win a lethal fight with a dominant.
- i = *resource inheritance*, or the probability of inheriting a valuable resource multiplied by the expected number of offspring that an individual will produce after it inherits the resource (relative to an established solitary individual). The probability of inheritance may largely depend on the differential survivorship of the dominant and the subordinate, whereas the expected number of offspring will depend primarily upon the relative value of the resource.
- p = the proportion of reproductive output, k, the subordinate obtains, or the inverse of reproductive skew.

Reeve and Ratnieks (1993) determine whether groups will form and the degree of reproductive skew by inserting the variables into an equation based on Hamilton's rule:

$$(P_m - P_n) + r(K_m - K_n) > 0 \tag{1}$$

This equation is formatted to highlight the conditions when one strategy (m) is favoured over another strategy (n) for an individual (P), and the above variables are appropriately inputted into this equation each time a subordinate or dominant is faced with two alternative decisions. The second half of equation (1) is the effect of P's strategy on individual K, or the indirect benefits of strategy m relative to n.

Complete skew

Reeve and Ratnieks (1993) first explore the necessary conditions for the subordinate to join the dominant when the subordinate receives no direct reproduction during the association ($p = 0$). Resource inheritance (i) is included to yield:

$$(i - x) + r(k - 1) > 0$$

This is rearranged to give:

$$x < r(k - 1) + i \tag{2}$$

Note that if $k = 1$ (i.e. there are no cooperative benefits), or if relatedness is zero, then

$$x < i \tag{3}$$

This means that a subordinate will join a dominant individual without any direct reproduction even if it receives no indirect benefits, provided that its expected reproductive success through resource inheritance is greater than its expected reproductive success through independent reproduction.

Under what conditions is a dominant individual expected to accept a subordinate? Using the same methodology as in equation (2):

$$xr < (k - 1) + ir \tag{4}$$

Again, if $k = 1$, then

$$xr < ir \tag{5}$$

showing that a dominant individual will allow a subordinate to join, provided that its indirect fitness gains via resource relinquishment (upon its death) to the subordinate exceed its indirect fitness gains derived from the subordinate's independent reproductive attempts. Note that if $r = 0$, then k should be greater than 1 for the subordinate's presence to be beneficial to the dominant.

'Staying incentives'

If $x > i$, the subordinate is expected to disperse. But the dominant could yield the subordinate some direct reproduction as a 'staying incentive' (*sensu* Reeve and Ratnieks, 1993). The minimum reproduction needed to 'induce' the subordinate to stay is given by:

$$p_s = [x - i - r(k - 1)]/k(1 - r) \tag{6}$$

The maximum reproduction the dominant is willing to relinquish is given by:

$$p_s = [k - 1 + r(i - x)]/k(1 - r) \tag{7}$$

The dominant is expected to provide a staying incentive when it can forfeit enough reproduction (equation 7) to make joining a profitable strategy for the subordinate (equation 6). Thus a staying incentive will be favoured when equation (7) > equation (6):

$$x - i < k - 1 \tag{8}$$

For the dominant to yield a staying incentive, k must be greater than 1. But because the subordinate gains i if it stays, the staying incentive, or p_s, is lower than in other RST models. If there are no cooperative benefits ($k = 1$), then the dominant will not provide a staying incentive and the subordinate should disperse (when $x > i$).

'Peace incentives'

If $x > i$, should the dominant yield a 'peace incentive' (*sensu* Reeve and Ratnieks, 1993)? A subordinate will be favoured to fight the dominant in a fatal battle when

$$f > x/(1 - r) \tag{9}$$

If $x < i$,

$$f > [i + r(k - 1)]/(1 - r) \tag{10}$$

If $k = 1$,

$$f > i/(1 - r) \tag{11}$$

If the conditions of (9), (10) or (11) are met, then a dominant should yield a peace incentive of

$$p_p = [f + r(1 - f - k) - i]/[k(1 - r)] \tag{12}$$

When $k = 1$,

$$p_p = f - i/(1 - r) \tag{13}$$

A dominant will yield a ‘peace incentive’ when $k = 1$, in contrast to withholding ‘staying incentives’ when $k = 1$. Resource inheritance reduces the proportion of reproduction a dominant will allow a subordinate, thus also decreasing the range of stable fighting conditions. That is, the greater chance that a subordinate will inherit the resources, the lower its willingness to fight for them.

Subordinate helping

Previous RST models (Vehrencamp, 1983a,b; Reeve and Ratnieks, 1993; Keller and Reeve, 1994; Reeve and Keller, 1995; Reeve, 1998; Reeve *et al.*, 1998) assumed that parameter k is fixed for a given group size. However, the value of k may vary with subordinate helping effort. Assuming k is under subordinate control, I explore the conditions when a subordinate is expected to help.

If $x < i$, a subordinate should help when

$$x < i(1 - s) < r(k - 1) \tag{14}$$

where s represents the cost of helping in the form of reduced survivorship. The subordinate is expected to help as long as the indirect benefits of helping outweigh the net decrease of i associated with the cost of helping (s). This is a simplification of the conditions favouring helping by the subordinate; clearly, many helpers in nature are unrelated to the recipients (but see ‘Queuing competition’ below). A more realistic treatment could allow i to increase with k, but for simplicity, here I assume the probability of inheriting resources is independent of helping, with the exception of the effect on survivorship.

Parental and sibling associations

Everything else being equal, Reeve and Keller (1995) demonstrate that parental associations should have relatively greater skew than sibling associations because of relatedness asymmetries. An offspring should be indifferent to rearing full siblings as opposed to its own offspring, since the relatedness coefficient in each case is 0.5, leading to an r value of 1 in RST models. In contrast, an individual in a sibling association will prefer to rear its own offspring as opposed to its sibling’s offspring, because of the higher relatedness coefficient. Emlen (1996) suggests age-effects of dominance as an alternative mechanism for observing greater skew in parental associations. I suggest resource inheritance as a third possible mechanism, which will further reinforce relatively greater skew in parental associations.

The parameter i in the above model is the probability of inheriting resources times the value of those resources. Differential survivorship between a dominant and a subordinate will affect the probability of inheritance. Due to age-specific differences alone, a parent may be more likely to die than a sibling, particularly if that sibling is in the same cohort. Therefore, everything else being equal, the inheritance parameter can be relatively greater in parental associations, thus leading to higher skew than found in sibling associations.

Queuing competition

When $x < i$ and $f < i$, queuing is the preferred strategy. However, in this two-breeder model, only a single inheritance slot is available. Assuming the dominant controls whether a subordinate can join, a dominant should accept a subordinate in the highest possible relatedness class to maximize its indirect benefits. Indeed, a dominant can incur a 'choosiness' cost (z) to insure it obtains a relative:

$$z < (k - 1) + r(i - x) \tag{15}$$

If $k = 1$,

$$z < r(i - x) \tag{16}$$

If $r = 0$,

$$z < (k - 1) \tag{17}$$

A dominant may still incur a cost to obtain (or maintain) an unrelated subordinate as long as the cost is lower than the cooperative benefits gained.

Whether this permitted cost will be in the form of direct reproduction transferred from the dominant to the subordinate will depend both upon the magnitude of cooperative benefits (k) and the number of subordinates available to queue. In saturated habitats, it is probable that subordinate individuals are not limiting, and that a dominant does not engage in a 'bidding game' (*sensu* Reeve, 1998) with other dominants; rather, a subordinate can enter a 'bidding game' with other subordinates for dominant acceptance by helping. Indeed, this perspective can shed light on many acts of helping found in nature. This idea is in line with Gaston's (1978) notion of helping as a type of payment to remain on a territory; that is, dominants may evict subordinates that do not help in favour of those that do. Equation (14) can be modified to relate i, or rather the probability of dominant acceptance, with subordinate helping (k).

DISCUSSION

Resource inheritance is common and widespread (Emlen, 1991). The prevalence of this phenomenon is due to the fact that resources necessary for successful reproduction may often outlive their owners. Indeed, the potential for resource inheritance exists when there is some risk of death and resources are transferable. Resource inheritance is not restricted to social organisms, as natal philopatry occurs in many solitary species, including reptiles (Reinhold, 1998), insects (Endo and Endo, 1993) and mammals (Waser, 1988). Therefore, the opportunity to inherit a valuable resource can influence dispersal decisions, thus setting the stage for further social evolution (Stacey and Ligon, 1987; Myles, 1988; Waser, 1988). There are many types of resources that can be transferred from one individual to another. Common examples include nests, territories, foraging grounds, oviposition sites, breeding slots or mates, food stockpiles, burrow systems, symbionts or other mutualists, predator refuges, and even helpers or workers.

The perspective that resource inheritance is an important factor influencing social organization is not novel. In addition to the vast empirical support for this phenomenon (see Stacey and Ligon, 1987; Myles, 1988; Emlen, 1991), there has also been much theoretical work on this issue (e.g. Brown, 1974, 1987; Woolfenden and Fitzpatrick, 1978; Bartz, 1982; Wiley and Rabenold, 1984; Lindström, 1986; Stacey and Ligon, 1987; Myles, 1988; Waser, 1988; Zack, 1990; Koenig *et al.*, 1992; Poiani, 1994; Ens *et al.*, 1995; Lucas *et al.*, 1997; Kokko *et al.*, 1998). Myles (1988) argued that resource inheritance was a primary selective factor that favoured the evolution of the soldier class in termites. Similarly, that inheritance of social rank affects the sex ratio at birth of both high- and low-ranking individuals is well documented in red deer *Cervus elaphus* (Clutton-Brock *et al.*, 1984) and several primate species (Symington, 1987; van Schaik and Hrdy, 1991). Furthermore, resource inheritance has been suggested to favour the evolution of environmental sex determination in reptiles (Reinhold, 1998), dispersal in relation to maternal senescence (Hamilton and May, 1977; Ronce *et al.*, 1998), guarding behaviour in the allodapine bee *Exoneura robusta* (Bull *et al.*, 1998), the evolution of female but not male workers in the Hymenoptera (Bartz, 1982), the occurrence of polydomy in ants (Rosengren and Pamilo, 1983) and lekking dynamics (Kokko *et al.*, 1998).

Given that reproductive skew theory is being widely tested and is suggested to be a ‘unified’ theory of social evolution (e.g. Sherman *et al.*, 1995), it is appropriate to consider the theoretical implications of including the common, but often neglected, phenomenon of resource inheritance. Inclusion of resource inheritance, a form of future direct (and indirect) benefits, allows the somewhat restrictive assumption of cooperative benefits to be relaxed. This extension increases the range of social systems to which RST may be applied, since some cooperative breeding studies have failed to demonstrate that helpers actually help (Ligon and Stacey, 1989; Emlen, 1999). Furthermore, it is unclear whether the cooperative benefits assumption holds in recent studies of skew theory (e.g. McRae, 1996; Jamieson, 1997; Whittingham *et al.*, 1997) or in other studies reviewed in light of skew theory (Keller and Reeve, 1994; Reeve *et al.*, 1998). Indeed, Clutton-Brock (1998) addresses the cooperative assumption as a key weakness of skew theory.

Reproductive skew theory has also been criticized for its notion of a ‘social contract’ (e.g. Clutton-Brock, 1998). Although I incorporated the assumption of dominant control (over subordinate reproduction) in the model presented here, resource inheritance diminishes the need for a ‘social contract’ in so far as the inheritance payoff to a subordinate may often be out of the control of a dominant. That is, the dominant can control whether to accept a subordinate but the inheritance payoff is largely a consequence of the dominant’s death. Thus the problem of dominant cheating (i.e. accepting help but not yielding reproduction) is reduced when subordinates are queuing for resources. Stable associations can therefore persist over a greater range without invoking a ‘social contract’.

In addition to relaxing the cooperative benefits assumption and diminishing the need for a ‘social contract’, the inclusion of inheritance also alters several of Reeve and Ratnieks’ (1993) qualitative predictions as highlighted below.

1. Complete skew can be stable when the subordinate receives no kin selected benefits. This result is quite common in systems where females are limiting and males cooperate for mate acquisition, such as cooperative polyandry or leks, and females represent a resource which may be inherited. Complete skew, low or zero relatedness, and female inheritance have been documented in pied kingfishers *Ceryle rudis* (secondary helpers; Reyer, 1984), long-tailed manakins *Chiroxiphia linearis* (McDonald, 1989), riflemen *Acanthissitta chloris* (Sherley, 1990) and boat-tailed grackles *Quiscalus major* (Poston, 1997). Prediction (1) is also exhibited in cooperatively breeding systems of dwarf mongooses *Helogale parvula* (Rood, 1990), green woodhoopoes *Phoeniculus purpureus* (Ligon and Ligon, 1978) and carpenter bees *Xylocopa sulcatipes* (Stark, 1992).
2. As emphasized above, stable associations may occur even when skew is complete and cooperative benefits are absent. This is found in many cooperative breeders where helpers

exert no beneficial effects on breeders' reproductive output, for example, jungle babblers *Turdoides striatus* (Gaston, 1978), green woodhoopoes *Phoeniculus purpureus* (Ligon and Ligon, 1990), red-cockaded woodpeckers *Picoides borealis* (Walters, 1990) and splendid fairy-wrens *Malurus splendens* (Russell and Rowley, 1990).

3. Dominants can incur a cost by associating with a queuing individual, even when cooperative benefits are absent, provided the subordinate is a relative. It is reasonable to suppose that lodging a queuing individual detracts resources that could have otherwise been allocated to a dominant's direct reproduction. This cost can be interpreted as a form of extended parental care, or investment towards future indirect benefits. Brown and Brown (1984) termed this phenomenon 'parental facilitation'. This perspective rotates the 'parental parasitism' hypothesis for the evolution of eusociality (Charnov, 1978) by 180°, whereby non-breeders are maximizing their future direct benefits and breeders are maximizing their future indirect benefits, as opposed to the reverse relationship operating in the present. Thus a form of 'offspring parasitism' can occur when queuing relatives remain on parental territories (see Brown, 1987; Poiani, 1994).

4. Dominants will only permit a cost of maintaining an unrelated queuer when co-operative benefits are present (if subordinate relative fighting abilities are negligible). The pied kingfishers *Ceryle rudis* illustrate this prediction, since breeding males will only accept unrelated helpers when subordinate help is beneficial (Reyer, 1980). Furthermore, because dominants will accept a relative if $k = 1$, but not a non-relative, everything else being equal, an unrelated subordinate will be more likely to help than a related subordinate. This is counter-intuitive to classic inclusive fitness arguments for the evolution of helping. Yet non-relatives provide more help than relatives in dwarf mongooses *Helogale parvula* (Rood, 1990). This prediction also supports Gaston's (1978) idea of helping as a form of rental 'payment'.

5. Dominants will prefer to associate with individuals in the highest available relatedness class. This prediction is a direct consequence of the indirect benefits a *dominant* will gain by relinquishing valuable resources to a related subordinate. This result also reinforces Reeve and Ratnieks' (1993) prediction that dominants will choose to associate with the highest related individual, since maximal skew can be imposed on relatives, given that the *subordinate* will gain indirect benefits. Yet Reeve and Ratnieks' prediction does not hold true when cooperative benefits are absent, whereas the resource inheritance prediction holds irrespective of the presence or absence of cooperative benefits. Depending on ecological conditions, pied kingfishers *Ceryle rudis* sometimes engage in a 'two-breeder' system (i.e. breeding pairs only accept one helper) and pairs prefer relatives over non-relatives (Reyer, 1980).

6. Intuitively, a 'staying incentive' (*sensu* Reeve and Ratnieks, 1993) will be favoured only when cooperative benefits are present. This represents a classical mutualistic relationship, whereby the dominant gains direct benefits through the subordinate's help; similarly, the subordinate gains direct benefits by associating with a dominant.

7. Everything else being equal, the extent of a 'staying incentive' is lower when resource inheritance is high. This prediction suggests that skew will be greater in associations where the dominant experiences a relatively higher mortality risk or when the resource is relatively more valuable. One possible test of this prediction is that helping subordinates should achieve a greater proportion of reproduction on *low*-quality territories or nesting substrates relative to *high*-quality territories or nesting substrates when $x > i$ and $k > 1$.

8. A general prediction resulting from the inclusion of resource inheritance is that, everything else being equal, skew can be higher in parental associations than in sibling associations. Higher skew can result from age-specific effects of mortality, which increases the probability of inheritance, or, rather, decreases the duration of the queue. This prediction reinforces Reeve and Keller's (1995) prediction of relatively higher skew in parental associations resulting from the relatedness asymmetries in parental and sibling associations, and Emlen's (1996) suggestion that skew may be greater in parental associations as a result of age-related dominance effects. One example of higher skew in a parental association than a sibling association comes from carpenter bees *Xylocopa* that inherit nesting substrates; Camillo and Garofalo (1989) determined that reproduction was evenly shared when sisters associated with one another, but reproduction was monopolized by the mother in parental associations.

9. 'Peace incentives' (*sensu* Reeve and Ratnieks, 1993) can be offered even when cooperative benefits are absent (unlike staying incentives) and when the probability that a subordinate will win a fight is high. Failed usurpations can result in peace incentives. For example, oystercatchers *Haematopus ostralegus* (Heg and van Treuren, 1998), pukekos *Porphyrio porphyrio* (Jamieson, 1997) and moorhens *Gallinula chloropus* (McRae, 1996) appear to fit this category, given that reproduction is shared and there is no evidence of cooperative benefits. Consistent with prediction (8), fighting abilities appear to be evenly matched in these systems. Furthermore, Heg and van Treuren (1998) determined that the only plausible explanation for adaptive cooperation in oystercatchers *Haematopus ostralegus* were future direct benefits gained from a greater probability of territory acquisition, or a form of resource inheritance.

However, it is unclear whether associations are stable in the case of failed usurpations. An alternative explanation for cooperation in these systems is simply a stalemate between two evenly matched competitors which go about reproducing as usual, but because of nesting limitations, collectively do not produce any more surviving offspring than solitary breeders. The relatively lower reproductive output each experiences may be tolerated, since it is better than the alternative of zero reproduction. A resident in these instances would have greater reproductive output as a single breeder, but presumably could not expel the intruder. Cant (1998) provides an alternative RST model without dominant control that may explain reproductive skew resulting from possible failed usurpations.

10. If helping, or cooperative benefits (k), is not a fixed value, and its value is under the control of a subordinate, then related subordinates will help as long as the indirect benefits derived outweigh the concurrent decrease in future direct benefits (i.e. inheritance probability) resulting from decreased survivorship or fecundity. Consistent with this prediction, a 'lazy worker' phenomenon occurs in naked mole-rats *Heterocephalus glaber* (Reeve, 1992), whereby the indirect benefits gained by helping relatives may not compensate for the corresponding loss of future direct benefits.

When inheritance slots are few and potential subordinates are many, subordinates may help to gain acceptance by dominants. When helping significantly increases the reproductive output of a dominant, and the dominant can choose between helping and non-helping subordinates, choosy dominants will be favoured over non-choosy dominants. One possible mechanism for dominant enforcement of subordinate helping is that a dominant can detect non-helpers and simply evict them. From prediction (4), helping effort should increase with decreasing relatedness if helping is used as an acceptance strategy by the subordinate.

Helping as an acceptance strategy is contrary to Reeve's (1998) conclusions regarding a 'bidding game'. Reeve assumes that the helping parameter (k) is fixed, and that dominants compete with one another (in the extent of direct reproduction they will allow the subordinate) to gain assistance from subordinates. This idea has theoretical appeal, and may occur when ecological constraints are low, but under conditions of high ecological constraints, competition among subordinates is more likely to result. For example, secondary helpers in pied kingfishers *Ceryle rudis* attempt to help many breeding pairs, but remain in the first group that accepts them (Reyer, 1980). Moreover, I suggest that mechanisms enforcing subordinate help (either help or be evicted) are easier to achieve than mechanisms that could possibly enforce the dominant's forfeiture of reproduction to subordinates.

The RST model presented here considers only two-breeder systems. However, dominance hierarchies, either based upon age or intrinsic abilities, among queuing subordinates are commonly found in nature (Gaston, 1978; Wiley and Rabenold, 1984; Chapais, 1988; Harcourt and Stewart, 1989; von Siemens, 1990; Poston, 1997; Kokko *et al.*, 1998). There is substantial evidence that the highest ranked subordinate obtains breeding status upon the death of the reigning dominant (e.g. Rood, 1990; Poston, 1997; Queller *et al.*, 1997). But upon the disappearance of a dominant, the dominant may be unable to determine its replacement. Therefore, a helping strategy to attain dominant acceptance into a group may not translate *per se* into the subordinate's queuing position within the group. This may help to explain why high-ranking subordinates often do not help (the expected payoffs of inheritance outweigh the expected gains through helping (prediction 3)) while lower-ranking subordinates do help (expected future direct reproduction is lower than expected present indirect benefits (prediction 3) or helping facilitates dominant acceptance). However, dominant interactions with subordinates may sometimes influence queuing rank (P. Nonacs, personal communication), and therefore, in some cases, it is possible that a subordinate may be able to rise in rank by increasing its helping effort. Clearly, there is variation between a subordinate's rank and its helping effort across social systems. Thus identifying the factors that determine subordinate rank (such as age, relatedness to the dominant or group, resource holding power, inheritance of maternal/paternal rank, time spent in the group, or helping effort) and correlating these factors with ecological conditions is an area where both theoretical and empirical studies will improve our understanding of social dynamics.

Although I have focused on resource inheritance (due to its widespread occurrence) as the mechanism of future direct benefits, there are clearly other forms of future benefits. For example, in saturated habitats, retained offspring commonly establish themselves in neighbouring territories upon vacancy (Walters *et al.*, 1988; Zack, 1990; Russell and Rowley, 1993). Emlen (1991) lists other avenues of future direct benefits, such as increased survival or obtaining parental experience. Mumme (1997) lists five avenues of future direct benefits; however, all but one, parental experience, fall into a broad classification of resource inheritance. Nonetheless, the parameter i presented here can correspond to *any* future direct benefits that accrue to a subordinate which chooses to associate with a dominant, such as increased survivorship to subordinates that delay dispersal. Accordingly, the predictions will remain the same, irrespective of the form of benefits. In addition, the inclusion of resource inheritance to RST is a channel of future indirect benefits to dominants. Thus the addition of the resource inheritance parameter i to RST accommodates Brown's (1980) four components of inclusive fitness – present direct and indirect benefits, and future direct and indirect benefits – and also attends to researchers' requests to consider future direct benefits as influencing delayed reproduction in cooperatively breeding species (Wiley and Rabenold, 1984; Stacey and Ligon, 1987; Poiani, 1994; Lucas *et al.*, 1997; Emlen, 1999).

Emlen (1991) has argued that differences between the habitat saturation hypothesis (Emlen, 1982) and the benefits of philopatry hypothesis (Stacey and Ligon, 1987), such as resource inheritance, are merely semantic, and that both hypotheses belong under the 'conceptual umbrella of ecological constraints'. If the aim is to obtain a broad conceptual understanding of the formation of social groups, then Emlen may be entirely correct in viewing the limitation of 'suitable habitats' as the primary mechanism favouring the retention of grown offspring, thus creating family groups subject to further social evolution. However, a single universal explanation, such as nesting limitations or ecological constraints, presents a limited tool kit for empiricists attempting to gain an understanding of factors potentially favouring sociality for a specific system. One appeal of RST is the reduction of variation into several empirically testable parameters. Again, such a general treatment may not apply to every social system, but it allows empirical studies to be conducted and compared using the same currency. I argue that a richer understanding of social systems will result if the 'conceptual umbrella' is put aside so that the consequences of searching for (or constructing) resources can be contrasted with the consequences of waiting for a resource. Although the value of the ecological constraints and resource inheritance parameters may both be influenced by similar factors (such as dominant mortality rates), waiting is a clear alternative to searching (or independent construction). Thus it is appropriate to define further the RST parameter of ecological constraints into two explicit categories: dispersal costs (or ecological constraints) and resource inheritance (or future benefits).

In conclusion, the potential for resource inheritance is a common natural phenomenon that may have a profound impact on both reproductive and dispersal decisions, thus affecting social structure and organization. Despite many papers suggesting the importance of inheritance to social systems, reproductive skew theory (Vehrencamp, 1983a,b; Reeve and Ratnieks, 1993; Keller and Reeve, 1994; Reeve and Keller, 1995; Reeve, 1998; Reeve *et al.*, 1998) does not explicitly include this factor as influencing the formation of social groups, or influencing the levels of skew found within social groups. Including resource inheritance yields novel predictions not found in other skew models, and these additional predictions appear to be met in many social organisms. Furthermore, classical RST does not explicitly include the life-history implications of present reproductive decisions on future reproduction. Although future subordinate reproduction could be perceived and calculated as lower overall skew and be incorporated into the model as such, to do so unnecessarily clouds both patterns and processes of social organization. Skew theory will be more transparent and more readily applied to real organisms when resource inheritance and other aspects of future inclusive fitness are included explicitly in the models and empirically tested.

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