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Models of reproductive skew: outside options and the resolution of reproductive conflict

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Summary

The two main types of skew models, transactional and compromise models, make different assumptions about the division of reproduction. Transactional models assume that one individual has full control over reproduction within the group, but may have to refrain from claiming all reproduction in order to prevent others leaving or evicting it from the group. Compromise models, by contrast, ignore outside options such as departing to breed elsewhere, but allow for incomplete control over reproduction within the group. Attempts to synthesize these two approaches have proved controversial. Here, we show that this controversy can be resolved using a simple principle from the economic literature on bargaining – the "outside option principle." Even if outside options are available, they will influence the outcome of reproductive conflict within a group only if they yield greater payoffs than are available within the group. We present a novel synthetic model based on this principle, in which individuals engage in a tug-of-war over reproduction within a group, but may "ease off" in their competitive effort in response to the threat of departure or eviction. We show that over a large range of parameter space, particularly when group productivity and relatedness among group members are high, these threats are not credible, so that opportunities outside the group do not influence the stable level of skew. However, when group productivity and relatedness are low, one or other of the players will typically ease off in competition in order to maintain group stability. Under these circumstances, outside

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options do influence skew. Tests which examine the relationship between skew and factors such as group productivity or ecological constraints are thus expected to yield variable results. The essential question is whether or not any of the members of a group stand to gain from its dissociation. The answer will determine whether or not outside options come into play.

Introduction

The term *reproductive skew* refers to inequality in the distribution of breeding success among members of a group (Vehrencamp 1983, Keller & Reeve 1994). In high-skew societies, such as those of honeybees (*Apis mellifera*), Mexican jays (*Aphelocoma ultramarina*), or meerkats (*Suricata suricatta*), the distribution of reproductive opportunities is markedly unequal (see, e.g., Chapter 13 in this volume). One or a few breeders monopolize reproduction, while others are denied the opportunity to mate or to raise offspring (and may even, in the case of eusocial insects or naked mole-rats (*Heterocephalus glaber*), develop as sterile workers). In low-skew societies, by contrast, all individuals have similar opportunities to breed (see, e.g., Chapter 15).

Inequality in breeding success is not a precisely defined concept. There are many different plausible ways in which to conceive and measure inequality in a multi-member group, leading to many different indices of skew (Kokko & Lindström 1997, Tsuji & Kasuya 2001). Moreover, inequality in actual reproductive success may be expected to arise simply by chance, even if all individuals have similar opportunities to breed (e.g. Haydock & Koenig 2002). Nevertheless, however one chooses to measure inequality, it is clear that there are dramatic and consistent differences in skew within and among species (Keller & Reeve 1994, Reeve & Keller 2001). Even closely related species otherwise similar in their ecology and behavior may differ markedly in this respect – compare, for instance, dwarf mongooses (*Helogale parvula*), in which typically only one female in a group breeds, with banded mongooses (*Mungos mungo*), in which most females breed in each attempt (Cant 2000). These differences in reproductive skew cry out for explanation.

Models of reproductive skew attempt to provide an adaptive account of variation in skew both between and within species. They assume that there exists a conflict of interest among members of a group, such that each would benefit by obtaining a greater share of reproduction than is in the best interest of the others. Each model then predicts how (at evolutionary equilibrium) this conflict of interest will be resolved, depending upon various factors such as the benefits of group membership, the opportunity for independent breeding, and the ability of each group member to compete for resources or breeding opportunities, as well as to evict or exclude others from the group (Reeve & Ratnieks 1993, Keller & Reeve 1994, Johnstone 2000).

Models of skew may differ in their assumptions about the extent of conflict between group members (e.g. Cant & Johnstone [1999] suggested that when production of offspring entails accelerating costs, individuals might all benefit from sharing reproductive opportunities). Most, however, are distinguished by their assumptions about the relative power of dominant and subordinate individuals. The most striking contrast in this respect is between transactional and compromise models of skew.

Transactional models of skew

Transactional models of skew were the first to be developed. Vehrencamp's (1979, 1983) seminal papers, in which she introduced the concept of reproductive skew, were built around a transactional model, and it is this approach that has been followed in most later analyses (e.g. Reeve & Ratnieks 1993, Johnstone & Cant 1999, Buston *et al.* 2007). In fact, when biologists talk of skew theory it is usually the transactional approach that they have in mind. The basic assumption of transactional models is that animals may concede reproductive opportunities to others, despite being potentially able to claim these opportunities for themselves, in order to maintain the stability of the group. This is advantageous because cooperation is presumed to yield productivity benefits. It may therefore pay to yield some reproduction to others in order to gain (or continue to enjoy) the benefits of associating with them.

There are in fact two types of transactional model. Early analyses focused on reproductive concessions offered by dominants to retain helpful subordinates in the group – in these models, dominance takes the form of complete control over reproduction, with dominant individuals yielding breeding opportunities to subordinates so as to make it worth their while remaining in the group rather than departing (Vehrencamp 1979, 1983, Reeve & Ratnieks 1993, Reeve & Emlen 2000). By contrast with this notion of "concessions," the "restraint" model focuses on reproductive concessions offered by subordinates to prevent the dominant evicting them – in these models, dominance takes the form of control over group membership, with subordinates refraining from claiming as large a share of reproduction as they might, lest the dominant eject them from the group (Clutton-Brock 1998, Johnstone & Cant 1999).

Both types of model can be formalised in a similar way (Reeve & Ratnieks 1993, Johnstone & Cant 1999, Johnstone 2000, Buston *et al.* 2007). Consider a pair of individuals, related by a coefficient r. In association, the combined reproductive success of the pair, relative to that of an established lone breeder, opportunities, as well as to evict or exclude others from the group (Reeve & Ratnieks 1993, Keller & Reeve 1994, Johnstone 2000).

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In the concession model, one "dominant" individual is assumed to have complete control over the distribution of reproduction within the group, subject only to the threat of departure by the "subordinate." In this case, the *subordinate* in a stable group is expected to receive the minimum share of reproduction, $p_{\min}$, that is compatible with group stability, i.e. a share that is just sufficient to ensure that leaving is not profitable. This share is given by

$$(kp_{\min} - d) + r(k(1 - p_{\min}) - 1) = 0 \tag{1.1}$$

where the first term on the left-hand side represents the direct fitness impact of staying (rather than leaving) on the subordinate, and the second term the indirect fitness impact on the reproductive success of the dominant. Rearranging, we obtain

$$p_{\min} = \frac{d - r(k - 1)}{k(1 - r)} \tag{1.2}$$

(if $d < r\,(k - 1)$, then the subordinate does best to remain even if the dominant completely monopolizes reproduction).

In the restraint model, by contrast, the "subordinate" is free to claim unsanctioned reproduction, subject only to the threat of eviction by the "dominant". In this case, the *dominant* is expected to receive the minimum share of reproduction, $q_{\min}$, that is compatible with group stability, i.e. a share that is just sufficient to ensure that evicting the subordinate is not profitable. This share is given by

$$(kq_{\min} - 1) + r(k(1 - q_{\min}) - d) = 0 \tag{1.3}$$

where the first term on the left-hand side represents the direct fitness impact of tolerating the subordinate's presence (rather than evicting it from the group) on the dominant, and the second term the indirect fitness impact of toleration on the reproductive success of the subordinate. Rearranging, we obtain

$$q_{\min} = \frac{1 - r(k - d)}{k(1 - r)} \tag{1.4}$$

In both models, the association will prove stable provided that

$$p_{\min} + q_{\min} < 1 \tag{1.5}$$

i.e. provided that the pair are together sufficiently productive that both may simultaneously receive at least their minimum required share. Substituting Equations 1.2 and 1.4 into 1.5, this yields the condition

$$1 + d < k \tag{1.6}$$

implying that the association will prove stable provided that the total productivity of both individuals would be reduced if it were to break up.

Concessions and restraint

From Equations 1.2 and 1.6, we see that in the concession model the subordinate's share of reproduction in a stable group increases with the opportunity for independent breeding (d), but decreases with the productivity of the group (k) and the degree of relatedness between the players (r). This makes intuitive sense – when there are greater benefits to be obtained elsewhere, the subordinate must receive a greater share of group productivity to make staying worthwhile; at the same time, the greater the productivity of the group, and the greater the relatedness between the players, the smaller the share required to satisfy this requirement. From Equations 1.4 and 1.6, however, we see that in the restraint model, the *dominant's* share exhibits precisely the same trends (with the exception that it decreases with the opportunity for independent breeding only for $r > 0$). Consequently, the two models generally yield opposite predictions regarding skew. For instance, when group productivity increases, the concession model predicts a decrease in the *subordinate's* share, leading to greater skew (provided that the dominant enjoys greater reproductive success than the subordinate). By contrast, the restraint model predicts a decrease in the *dominant's* share, leading to reduced skew (again provided that the dominant enjoys greater reproductive success than the subordinate).

The difference between the two models lies in the roles assigned to the two individuals. In the concession model, it is the subordinate that threatens to break up the group, and the dominant that must concede reproduction it could otherwise claim in order to maintain the association; in the terminology of Buston *et al.* (2007) it is the dominant that allocates reproduction to its partner. By contrast, in the restraint model it is the dominant that threatens to break up the group, and the subordinate that must concede reproduction; in this case it is the subordinate that is the allocator. The terms "dominant" and "subordinate" thus carry different meanings in the two models. In the concession model, dominance denotes control over the division of reproduction (subject to the threat of departure by the subordinate), while in the restraint model, dominance denotes control over group membership (i.e. the power to evict).

Compromise models

The concession and restraint models yield opposing predictions about skew, but both are instances of the transactional approach. In both, one individual is assumed to exercise full control over the division of reproduction, subject only to the threat of group breakup (which may be initiated by the other individual). Compromise models instead assume that each member of the group can act selfishly to claim a greater share of breeding opportunities, at a cost to the productivity of the group as a whole (Clutton-Brock 1998, Reeve *et al.* 1998, Johnstone 2000). The outcome of the conflict over reproduction depends upon the level of selfish effort invested by each individual, and on their relative "strength." In this kind of model, "dominance" typically takes the form of greater competitive ability – the dominant individual may be able to invest more effort in competition than can subordinates, or it may obtain a greater share for the same level of investment, due to superior resource-holding potential (Reeve *et al.* 1998). The other factor that can affect the outcome of the conflict in these models is relatedness among group members, which potentially influences the level of competitive effort that each individual will invest at equilibrium.

The most influential compromise model, the tug-of-war game of Reeve *et al.* (1998), focuses (like the simple transactional models described above) on the interaction between two individuals, one dominant and one subordinate, who are related by a coefficient r. Both players simultaneously choose how much effort to invest in selfish competition over reproductive opportunities within the group. The levels of effort will be denoted x for the dominant and y for the subordinate. Total group productivity is equal to $k(1-x-y)$, where the parameter k specifies group productivity relative to that of a lone breeder in the absence of competition. Productivity thus declines linearly with total expenditure by both players on selfish competition. The fraction of reproduction claimed by the dominant is equal to $x/(x+by)$, where the parameter b (<1) specifies the competitive ability of the subordinate relative to that of the dominant. Dominance in this context is thus defined by superior competitive ability.

Given the above assumptions, the direct fitness payoffs to the two players from the tug-of-war are given by

$$
\begin{aligned}
W_d(x,y) &= k(1-x-y)\frac{x}{x+by} \\
W_s(x,y) &= k(1-x-y)\frac{by}{x+by}
\end{aligned}
\tag{1.7}
$$

Reeve *et al.* (1998) derived the (unique) stable pair of effort levels x^* and y^* in the basic tug-of-war game, each of which simultaneously maximizes (for the player in question, given the other's behavior) the sum of its own direct fitness payoff plus r times that of the other player. These effort levels satisfy the first-order condition

$$
\frac{\partial W_d(x,y)}{\partial x} + r\frac{\partial W_s(x,y)}{\partial x} = \frac{\partial W_s(x,y)}{\partial y} + r\frac{\partial W_d(x,y)}{\partial y} = 0 \tag{1.8}
$$

and are given by

$$
\begin{aligned}
x^* &= \frac{b}{2(1-b)}\left[\frac{2-r(1-b)}{\sqrt{r^2(1-b)^2+4b}} - 1\right] \\
y^* &= \frac{1}{2(1-b)}\left[1 - \frac{2b+r(1-b)}{\sqrt{r^2(1-b)^2+4b}}\right]
\end{aligned}
\tag{1.9}
$$

The share of reproduction obtained by the subordinate at this equilibrium increases with its relative competitive ability, b, but surprisingly it is largely insensitive to the relatedness between the competitors, r. As relatedness increases, both players reduce their competitive effort, with the result that skew changes little.

Outside options

Much recent discussion of reproductive skew has focused on the issue of control. Can the dominant really prevent subordinates from claiming any share of reproduction, as concession models assume? Or are subordinates able to gain some reproductive success even against the best interests of the dominant, as in compromise models?

Can subordinates even claim a large enough share that the threat of eviction becomes relevant? Framed in these terms, compromise and transactional approaches start to seem less clearly distinct. Perhaps concession and restraint models simply represent extreme cases on a continuum of dominant control – the former deal with cases in which the dominant has full control over reproduction, the latter with cases in which the dominant has none (except that granted by the threat of eviction).

There remains, however, another fundamental difference between transactional and compromise models. The transactional models incorporate *outside options* – the possibility of leaving to breed elsewhere, or of evicting a competitor from the group. Indeed, it is these outside options that, in transactional analyses, set limits on the level of skew possible in a stable group. The fitness prospects of individuals that leave or are forced out of a group, usually referred to in terms of ecological constraints, thus have a major influence on skew in transactional analyses. By contrast, compromise models have generally ignored outside options, and focus only on the resolution of conflict within the group. Ecological constraints thus have no influence on the outcome of these analyses.

In reality, it seems likely that animals will often have the opportunity to leave a group and breed elsewhere, or to evict others from the association. But at the same time, it also seems likely that no one individual will enjoy complete control over reproduction within the group. A realistic model of skew, therefore, needs to incorporate both competition over reproduction within the group, as in compromise models, and outside options, as in transactional models. How are these two approaches to be combined? While there have been several attempts to "synthesize" skew models in order to answer this question, there is still little agreement over which approach is appropriate (Johnstone 2000, Reeve & Shen 2006, Nonacs 2007).

Synthetic models

In a previous review paper (Johnstone 2000), one of us outlined a synthetic model of skew that attempted to incorporate outside options into the tug-of-war model of Reeve *et al.* (1998). In this combined model, animals were assumed first to yield concessions to one another, in the form of uncontested shares of group productivity, sufficient to ensure that neither would benefit by leaving the group. Subsequently, both were assumed to engage in a tug-of-war competition over the remaining, contested fraction of reproduction. The model suffers from a problem, however, in that the concessions required to prevent departure in the first step are calculated on the basis of total group productivity, overlooking the fact that some of this productivity will be squandered in competition during the second step. Because of the costs of competition, the original concessions lose some of their value, and can no longer be relied upon to ensure group stability when the outcome of the tug-of-war is taken into account.

Reeve and Shen (2006) attempted to deal with this problem in a modified synthetic model. They too allow individuals to concede uncontested shares of reproduction to one another, and assume that a tug-of-war takes place over the remaining contested fraction. However, they assume that the magnitude of the concessions and the intensity of effort in the tug-of-war are decided simultaneously. Consequently, they suggest that an "evolutionarily stable" outcome must satisfy two simultaneous conditions: (1) each player must be just indifferent between remaining in the group and choosing its outside option, and (2) each player's competitive effort in the tug-of-war must be a best response to that of the other, given the magnitude of the concessions made by each (i.e. selfish efforts are at a Nash equilibrium). Once again, however, this approach seems to us problematic. First, it rests on the questionable assumption that the players use up all the potential benefits of group membership in the process of finding a resolution (see Nonacs 2007). Second, the putative solution is also based on the assumption that each player gives away a "free" share of reproduction to its opponent while simultaneously fighting hard for the remainder. Intuitively, it would make more sense for each player to reduce the size of the free share offered to its partner, and invest less effort in wasteful competition. This intuition is borne out by formal analysis – one can show that any solution of the form suggested by Reeve and Shen (2006) can be invaded by a mutant that offers a reduced "handout" and at the same time invests less in wasteful competition over the remainder.

Nonacs (2007) forcefully critiques both of the above models, highlighting some of the same problems we have pointed out here. He then presents results of a simulation analysis in which individuals may exchange shares of uncontested reproduction while simultaneously engaging in a tug-of-war over the remainder. The results are that such exchange always proves unstable, and that levels of competitive effort evolve to the solution of the basic tug-of-war game. However, since the analysis omits any possibility of departure or eviction, this is unsurprising. Removing all outside options renders concessions pointless, and the game merely reduces to the basic tug-of-war. The question thus remains, when outside options are available, when and how will this affect the outcome of competition over reproduction within the group? If the exchange of uncontested shares of reproduction (as proposed by Johnstone 2000 and Reeve & Shen 2006) is unfeasible or unstable, how should we expect competitors to respond to the threat of the group breaking up?

Bargaining theory and the outside option principle

A possible solution to the problem of synthesis can be gleaned from work in economic bargaining theory, which is concerned with problems that are structurally very similar to those addressed by models of skew (Nash 1950, Osborne & Rubinstein 1990, Muthoo 1999). In economics, a "bargaining situation" is one in which two or more players have a common interest to cooperate, but disagree over how the profits of cooperation should be distributed. An obvious example is trade, although formally similar problems arise in a range of other contexts, from salary negotiations and litigation to military disputes between nation states (Fearon 1995, Muthoo 1999, 2000, Powell 2002). There is a large literature on bargaining theory in economics which we will not attempt to review here; readers seeking an accessible introduction are directed to Muthoo (1999, 2000). Rather, we need only refer to a simple principle of bargaining theory, the "outside option principle" (Binmore 1985, Sutton 1986), to help solve the problem of how to synthesize models of reproductive skew.

The outside option principle suggests that a focal individual's outside option will influence the resolution of within-group conflict only if this option yields a greater payoff to the focal individual than the payoff it expects to receive through negotiation (Nash 1953). In these circumstances the individual can use a credible threat to exercise its outside option to obtain a more favorable resolution, one that is sufficient to render the threat incredible. The principle chimes with our everyday intuition about bargaining situations. Imagine, for example, a bartender earning $10 per hour who demands a raise from his employer on the grounds that the bar across the street is offering an hourly rate of $9. Clearly, a rational employer will be left unmoved by this threat of departure. Only if the other bar is offering more than $10 per hour will the employer need to take the threat seriously, and decide whether it is worth raising her own offer to retain the worker. Threats to take action that both parties know would be self-defeating are not credible, and so should exert no influence on the resolution of conflict (Nash 1953, Binmore 1985, McNamara & Houston 2002).

The outside option principle suggests that the models of Johnstone (2000) and Reeve & Shen (2006) encounter problems in part because they assume that players always concede shares of reproduction to one another, even under circumstances in which the threat of eviction and the threat of departure prove incredible. This conclusion was also reached independently by P. Buston and A. Zink, in an unpublished manuscript sent to us while this chapter was being written. In the next section, we apply the outside option principle to resolve these problems, and determine when and how the possibilities of departure and of eviction influence behavior in a tug-of-war over reproduction. The key difference between our approach and that of previous synthetic models is that, rather than start with the assumption that an equilibrium features concession of uncontested shares of reproduction, we first focus on the resolution of the tug-of-war, and then use this to determine whether concessions are necessary.

The model

We focus on the interaction between two individuals, one dominant and one subordinate, who are related by a coefficient r. Dominance in this context is defined by the ability to evict the subordinate from the local breeding territory, although we also allow for the possibility that the dominant may enjoy an advantage over the subordinate in competing for reproductive opportunities within the local territory. In the extreme, the dominant may enjoy complete control over reproduction.

The interaction involves two stages. In the first stage, both players simultaneously choose how much effort to invest in selfish competition over reproductive opportunities within the group. This stage is identical to the "tug-of-war" game of Reeve *et al.* (1998). The levels of effort will be denoted x for the dominant and y for the subordinate. Following the first stage, both players simultaneously choose whether to remain in association and accept the payoffs from the tug-of-war, or whether to terminate the interaction. If either player chooses to terminate the interaction, then we assume that the dominant retains control of the breeding territory and thus receives a direct fitness payoff of 1 (baseline productivity for a lone breeder), while the subordinate receives a direct fitness payoff of d (1), reflecting the cost or risk associated with locating alternative breeding opportunities. The "outside options" available to the players are thus departure for the subordinate, and eviction for the dominant (though when $d=1$ both players are indifferent as to who leaves and who stays).

Evaluation of outside options

The direct fitness payoffs to the two players from the tug-of-war, if both remain in association, depend upon the effort levels of both, and are given by

$$\begin{aligned} W_d(x,y) &= k(1-x-y)\frac{x}{x+by} \\ W_s(x,y) &= k(1-x-y)\frac{by}{x+by} \end{aligned} \tag{1.10}$$

In the second stage of the game, therefore, the subordinate stands to gain by departing if and only if

$$(d - W_s(x,y)) + r(1 - W_d(x,y)) > 0 \tag{1.11}$$

while the dominant stands to gain by evicting the subordinate if and only if

$$(1 - W_d(x,y)) + r(d - W_s(x,y)) > 0 \tag{1.12}$$

If neither condition is met, then both players do best to remain in association. Under these circumstances, neither the threat of departure nor the threat of eviction is credible.

Stable levels of competitive effort

How do the threats of departure and eviction in the second step of the game affect the players' choices of competitive effort during the first step? The (unique) stable pair of effort levels x^* and y^* in the basic tug-of-war game (derived by Reeve *et al.* 1998) were given above. If the resulting direct fitness payoffs to both players are great enough that neither condition (1.11) nor condition (1.12) is satisfied for effort levels x^* and y^*, then the stable outcome of the game is unaffected by the possibility of departure or of eviction, because neither threat is credible given the outcome of the tug-of-war. Only if one or both of the players stands to gain by departing or evicting the other will the availability of outside options influence the resolution of the conflict.

The "concession" zone

If

$$\begin{aligned}(1 - W_d(x^*,y^*)) + r(d - W_s(x^*,y^*)) &< 0 \\ &< (d - W_s(x^*,y^*)) + r(1 - W_d(x^*,y^*))\end{aligned} \tag{1.13}$$

then the dominant stands to gain from the association, while the subordinate does best (given effort levels x^* and y^*) to depart. Under these circumstances, the *dominant* must "ease off" in the tug-of-war if it is to retain the subordinate in the group. This potentially leads to what we shall call a "concession" equilibrium, at which the stable effort levels of the two players, denoted x_c and y_c, satisfy

$$\frac{\partial W_s(x,y)}{\partial y} + r\frac{\partial W_d(x,y)}{\partial y} = 0 \text{ for } x = x_c, y = y_c \tag{1.14}$$

and

$$(d - W_s(x_c,y_c)) + r(1 - W_d(x_c,y_c)) = 0 \tag{1.15}$$

Equation 1.14 implies that the subordinate does not stand to gain from a change in effort level, because this would entail a net decrease in the inclusive fitness payoff from the tug-of-war. Equation 1.15 implies that the dominant does not stand to gain from an increase in its effort, because this would trigger departure by the subordinate, which obtains an inclusive fitness from the tug-of-war that is just sufficient to make departure unprofitable. Such an outcome will, however, only prove stable provided that

$$(1 - W_d(x_c, y_c)) + r(d - W_s(x_c, y_c)) < 0 \tag{1.16}$$

If this condition is not met, then the dominant will not be selected to reduce its competitive effort in the tug-of-war sufficiently to retain the subordinate, since it would do better simply to evict its competitor.

The "restraint" zone

If

$$\begin{aligned}(1 - W_d(x^*, y^*)) + r(d - W_s(x^*, y^*)) > 0 \\ > (d - W_s(x^*, y^*)) + r(1 - W_d(x^*, y^*))\end{aligned} \tag{1.17}$$

then the subordinate stands to gain from the association, while the dominant does best (given effort levels x^* and y^*) to evict its competitor. Under these circumstances, the *subordinate* must "ease off" in the tug-of-war if it is to be allowed to remain in the group. This potentially leads to what we shall call a "restraint" equilibrium, at which the stable effort levels of the two players, denoted x_r and y_r, satisfy

$$\frac{\partial W_d(x,y)}{\partial x} + r\frac{\partial W_s(x,y)}{\partial x} = 0 \text{ for } x = x_r,\ y = y_r \tag{1.18}$$

and

$$(1 - W_d(x_r, y_r)) + r(d - W_s(x_r, y_r)) = 0 \tag{1.19}$$

Equation 1.18 implies that the dominant does not stand to gain from a change in effort level, because this would entail a net decrease in the inclusive fitness payoff from the tug-of-war. Equation 1.19 implies that the subordinate does not stand to gain from an increase in its effort, because this would trigger eviction by the dominant, which obtains an inclusive fitness from the tug-of-war that is just sufficient to make eviction unprofitable. Such an outcome will, however, only prove stable provided that

$$(d - W_s(x_r, y_r)) + r(1 - W_d(x_r, y_r)) < 0 \tag{1.20}$$

If this condition is not met, then the subordinate will not be selected to reduce its competitive effort in the tug-of-war sufficiently to be tolerated by the dominant, since it would do better simply to leave.

Group breakup

If the solution of the original tug-of-war model is unstable because one or other of the players stands to gain by exercising their outside option, but at the same time neither a concession equilibrium nor a restraint equilibrium is feasible, then we expect that the association will break up. An equilibrium at which $x < x^*$ and $y < y^*$, i.e. at which both players simultaneously "ease off" in the tug-of-war in order to maintain group stability, is not possible. If both players stand to gain from the outcome of the basic tug-of-war, then neither the threat of departure nor the threat of eviction is credible, so that neither player needs to adjust its effort level in response. Conversely, if neither player stands to gain from the outcome of the basic tug-of-war, then neither has any incentive to "ease off" in order to maintain an association that is unprofitable to both.

Results

We have derived analytical solutions for the boundaries of the regions of parameter space in which one obtains the different outcomes described above. Since these expressions are in some cases complex, we will not give them here; instead, Figures 1.1 and 1.2 show graphically these regions of parameter space, for the case of unrelated ($r = 0$) and related ($r = 0.5$) competitors, respectively. The general qualitative pattern is simple: groups are more likely to break up when productivity (k) is low, the opportunity for independent breeding (d) is great, and competitors are less closely related. Breakup is also more likely for an intermediate level of asymmetry in competitive ability between dominant and subordinate. There is a substantial region in which both the threat of departure and the threat of eviction prove incredible, so that the solution of the basic tug-of-war game is stable and unaffected by outside options. This outcome is most likely when group productivity is high, there is little opportunity for independent breeding, and competitors are more closely related. Once again, it is also more likely for an intermediate level of asymmetry in competitive ability between dominant and subordinate. When the subordinate is much weaker than the dominant, and particularly when there are substantial opportunities for independent breeding and the competitors are unrelated, the threat of subordinate departure becomes credible. Under these circumstances we obtain a "concession" equilibrium at which the dominant "eases off" in competition to retain the subordinate in the group. Conversely, when the subordinate is not too much weaker than the dominant, and again particularly when there are substantial opportunities for independent breeding and the competitors are unrelated, the subordinate may have to "ease off" in competition for its presence to be tolerated.

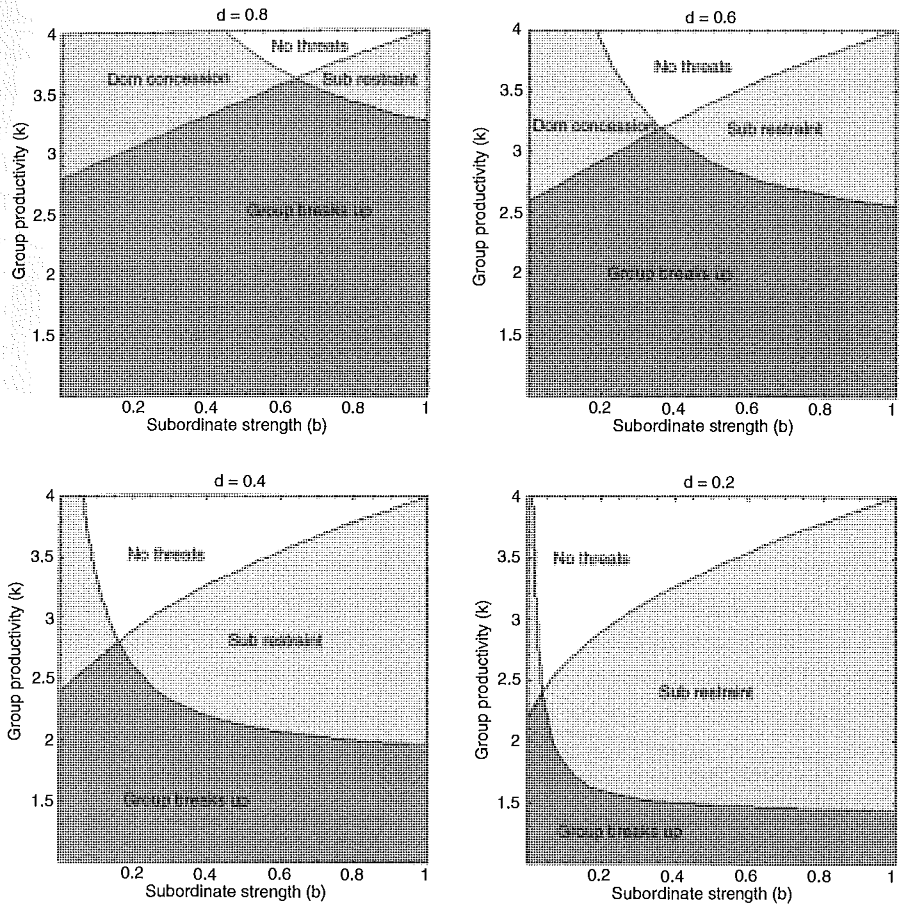

Figure 1.1 The graphs show, for unrelated players ($r = 0$), the regions of parameter space in which: (i) the solution of the basic tug-of-war game proves stable because both the threat of departure and the threat of eviction are incredible (labeled "no threats"); (ii) the dominant must reduce its competitive effort to prevent departure of the subordinate (labeled "Dom concession"); (iii) the subordinate must reduce its competitive effort to prevent eviction by the dominant (labeled "Sub restraint"); (iv) the association proves unstable. In each graph, the relative competitive ability of the subordinate (b) increases from left to right along the horizontal axis, and group productivity (k) increases from bottom to top along the vertical axis. Different graphs give results for different levels of opportunity for independent breeding (d): high opportunity in the top-left graph, and low opportunity in the bottom-right graph.

Implications for skew

What is the significance of these different solution regions? It matters in which region a population or species falls, because depending on the nature of the outcome, patterns of skew are expected to be very different. When

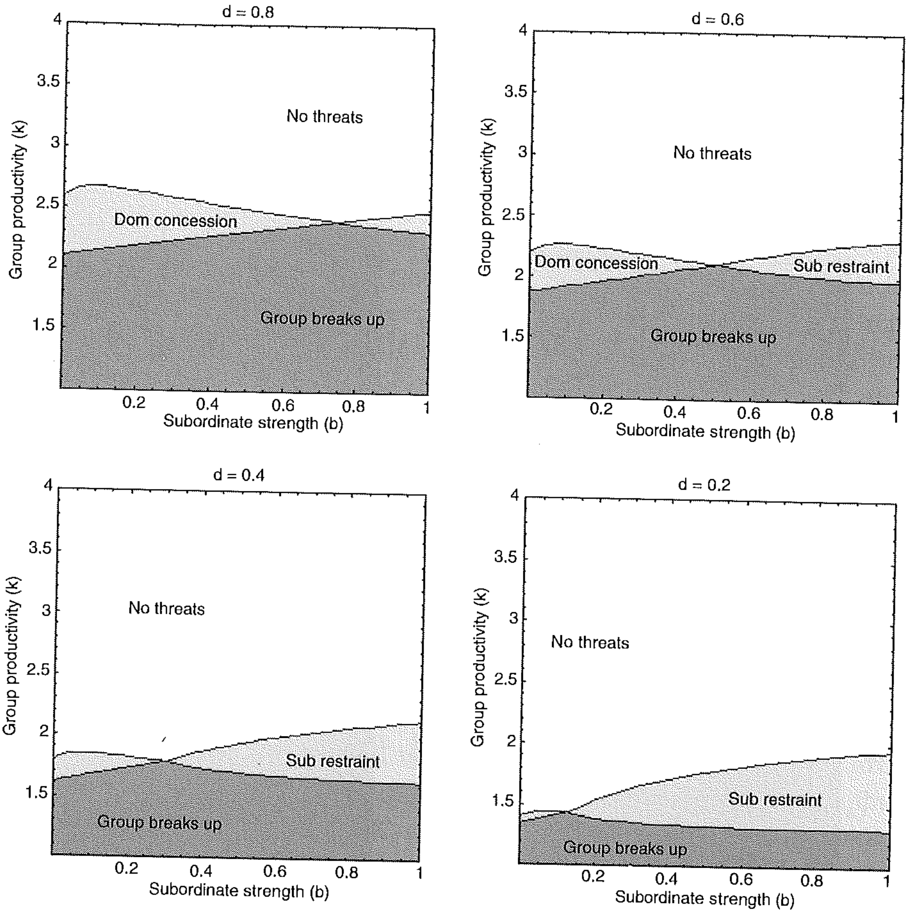

Figure 1.2 Regions of parameter space as in Figure 1.1, for related players ($r = 0.5$).

neither the threat of departure nor the threat of eviction is credible, outside options, as we have seen, do not come into play. Under these circumstances, neither ecological constraints nor the opportunity for independent breeding nor group productivity exert any influence whatsoever on the level of skew within a group. As mentioned previously, relatedness also has little influence on stable skew in the tug-of-war game, so that in this region the relative competitive ability of the subordinate will be the only significant influence on skew (with stronger subordinates gaining a greater share of reproduction).

Outside options typically come into play, as described above, when the subordinate is either very weak or very strong, group productivity is low, relatedness is low, and there are opportunities for independent breeding. In these "concession" and "restraint" regions, group productivity, relatedness, and the opportunity for independent breeding will influence the level of skew in a group, just as in simple transactional models of skew. In the concession region, where the dominant is forced to "ease off" in competition in order to retain the subordinate, the latter's share of reproduction will increase with the opportunity for independent breeding and decrease with group productivity and relatedness. By contrast, in the restraint region, where it is the threat of eviction that comes into play, the subordinate's share of reproduction will decrease with the opportunity for independent breeding and increase with group productivity. Lastly, across both concession and restraint regions, the subordinate's share increases with its competitive ability (just as in the basic tug-of-war).

Discussion

Taking account of the "outside option principle" leads to a synthetic model of skew that does not suffer from the stability problems of previous analyses. The threat of departure and the threat of eviction come into play only when they are credible; moreover, they lead to players "easing off" in competition, rather than exchanging uncontested shares of reproduction. The question of how individuals could possibly "agree" to refrain from competing over a proportion of the available reproductive opportunities does not, therefore, arise. The results suggest a rather different view of reproductive skew from previous attempts at synthesis.

While some have argued for the universal scope and power of transactional (particularly concession) models, and their potential for unifying the study of social evolution (e.g. Reeve & Keller 2001, Buston *et al.* 2007), the present analysis suggests that they are relevant only under certain restricted circumstances. Where group members are closely related and/or the productivity benefits of association are great, the threat of departure or of eviction is likely to prove incredible, because the direct and indirect benefits of group membership are too large to forgo. Under these circumstances, the whole basis of transactional skew models is eliminated. No concessions need be offered, because there is no opportunity for either player to gain by dissolving the association. Consequently, manipulating outside options is not expected to influence skew (see, e.g., Langer *et al.* 2004, Heg *et al.* 2006). Rather strikingly, these circumstances of high relatedness and high group productivity are precisely those in which selection is most likely to favor association in the first place. Consequently, the most obviously beneficial interactions are those least likely to be amenable to analysis in terms of skew theory.

Should we then abandon skew models completely? We would argue not. The burgeoning literature on biological markets and partner choice (Noë *et al.* 1991, Noë & Hammerstein 1994, Bshary & Noë 2003, Sachs *et al.* 2004, Foster & Wenseleers 2006) attests to a growing awareness among biologists that outside options are often important. Although most of the classical applications of game theory in biology focus on "forced play" among a small number of players, there are many situations in which one individual is not forced to interact with another, but can readily switch partners or perhaps forgo any interaction at all. Under these circumstances, it is not surprising that the threat of terminating an interaction and losing a partner should exert a significant influence on behavior within the association. Such "sanctions" have become the focus of much discussion in the study of mutualism and cooperation (see, e.g., Herre *et al.* 1999, Ferrière *et al.* 2002, Johnstone & Bshary 2002, West *et al.* 2002, Bshary & Noë 2003, Kiers *et al.* 2003, Sachs *et al.* 2004, Foster & Wenseleers 2006), and an elegant experimental demonstration is provided by studies of interaction between cleaner-fish and clients, in which the threat of departure by the client induces cleaners to refrain from biting live tissue (Bshary & Grutter 2002, 2005). Although this example may seem rather remote from reproductive skew, it illustrates the same principle that lies at the heart of skew theory – that individuals' prospects *outside* a given association can influence the resolution of conflicts *inside* it.

The key feature of biological "markets" that renders the threat of departure (or rejection) credible is the ready availability of alternative partners. We suggest, accordingly, that transactional skew theory is likely to prove most relevant not to highly profitable associations involving small numbers of closely related individuals, who may have little opportunity to join a similar family group elsewhere, but to looser and less cooperative associations between more distantly related individuals. Individuals in such cases may have opportunities to move between alternative, unrelated groups, so that the threat of departure may become credible, just as the threat of eviction may when group members can be easily replaced or contribute little to productivity in any case. Indeed, it is surprising that, apart from some work by Reeve (1998), there has so far been little attempt to incorporate market effects explicitly into skew theory.

The response of other group members to the prospect of departure or an attempt at eviction need not, as our model shows, involve the "exchange" of uncontested shares of reproduction, with all of the questions this raises about how animals might achieve such a feat, and what prevents cheating. Individuals may simply reduce their competitive efforts in response to the risk of triggering the breakup of a group. To detect such influences is likely to be difficult, because an effective threat is precisely one that elicits responses that make it unprofitable to carry out. Consequently, social behavior might potentially be influenced by many "invisible" threats that remain hidden until the "rules" they enforce are broken. However, threats of this kind can be exposed by experimentally staging such violations. Wong *et al.* (2007), for instance, have shown that the typical size hierarchy seen in groups of the coral-dwelling goby *Paragobidon xanthosomus* is maintained by the latent threat of eviction: when dominant fish were experimentally paired with subordinates larger than observed under natural circumstances, eviction was the result (while dominants tolerated individuals who were smaller than themselves).

Conclusion

To sum up, we suggest that outside options can influence the resolution of reproductive conflict within a group, but that they will do so only when the threat of departure or of eviction is credible. Consequently, tests which examine the relationship between skew and factors such as group productivity or ecological constraints are expected to yield variable results. The essential question is whether or not any of the members of a group stand to gain from its dissociation. The answer will determine whether or not outside options come into play.

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