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REVIEW

A tale of two theories: parent–offspring conflict and reproductive skew

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The recent development of reproductive skew (RS) theory shows striking parallels with that of parent–offspring conflict (POC) theory a decade earlier. In particular, the concept of 'battleground' and 'resolution' models in POC theory is equally relevant to RS theory. The battleground of conflict in POC and RS has been defined by different constraints (which I term 'optimization' and 'group stability' constraints, respectively). This distinction is not inherent but arises simply because POC models assume that the fitness benefits of an increasing share of resource show diminishing returns, whereas skew models assume a linear relation between reproductive share and fitness. Incorporating diminishing returns into skew models reveals a simple and almost wholly neglected explanation for reproductive sharing. Models of POC have moved on from simply defining the battleground to consider how conflict within it is resolved. The development of analogous models for RS theory is at a relatively early stage. In particular, more work is needed to understand the manner and extent to which overt aggression can mediate reproductive control. Lessons learned from attempts to test POC theory can help guide tests of RS theory, and provide information on both the nature of the battleground over reproduction and the mechanism by which conflicts are resolved.

The last decade saw a surge of interest in the study of reproductive skew, which measures the evenness with which reproduction is shared between group members in cooperative animal societies. The reasons for this interest are at least three-fold. First, there is something conspicuous to explain. Recent advances in genetic technology have revealed great variation at both interspecific and intraspecific levels in the degree to which dominant individuals monopolize reproduction, from low-skew societies, in which all or most group members breed, to high-skew societies in which only dominant individuals reproduce directly (Keller & Reeve 1994). Second, inequalities in reproductive share translate more or less directly into inequalities in direct fitness, so that game-theoretical models can be used as investigatory tools without recourse to questionable assumptions about the trade-offs involved, or how the currency being optimized converts to fitness. Finally, many researchers were drawn to work on reproductive skew because theory was based on a simple, general model which, if substantiated, implied that patterns of social evolution across diverse taxa could be explained by a few key genetic and ecological parameters (Vehrencamp 1979, 1983; Emlen 1982; Reeve 1991; Reeve & Ratnieks 1993).

In recent years, however, some of the initial optimism and enthusiasm for skew theory has waned. A number of alternative models have been proposed which are based on distinct mechanisms but nevertheless generate similar or overlapping predictions (Cant 1998; Reeve et al. 1998; Cant & Johnstone 1999; Johnstone & Cant 1999a; Kokko & Johnstone 1999; Ragsdale 1999; Crespi & Ragsdale 2000; Reeve 2000; Cant & Reeve 2002; Kokko 2003). At the heart of this theoretical dispute is a simple issue: power (Clutton-Brock 1998; Beekman et al. 2003). Given conflicting interests between dominant and subordinate, which individual will win? This debate will be familiar to students of another exciting theory in behavioural ecology: parent–offspring conflict (POC). Here the question is which party, parents or offspring, will win the conflict over parental investment? Indeed, the recent development of skew theory shows striking similarities to the historical course of parent–offspring conflict theory a decade earlier. Some of the lessons learned from POC are directly relevant to evolutionary conflict over reproduction. In

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particular, the concepts of 'battleground' and 'resolution' models in POC can be applied to skew theory to gain a better understanding of the aims, uses and limitations of the models, and insights from POC can shed new light on patterns of social aggression and overt conflict in animal societies.

DEFINING THE BATTLEGROUND

Trivers (1974) proposed that conflict will exist between parents and offspring over the level of parental investment (PI) because parents place equal genetic value on their offspring whereas an individual offspring values itself over its siblings. This reasoning was immediately challenged by Alexander (1974) who argued that any advantage gained by an offspring from its parent would rebound as a cost when the offspring became a parent itself. The debate was resolved a few years later when population genetic models were used to show that 'conflicting' alleles which cause an offspring to demand extra PI from its parents can spread at the expense of 'nonconflicting' alleles at the same locus (Macnair & Parker 1978, 1979; Parker & Macnair 1978, 1979). Where offspring gain diminishing returns from increasing parental investment, both parents and offspring favour some optimal level of PI, but this optimum is higher from the perspective of the offspring than from that of the parent. The parental optimum sets a lower bound on the level of PI that will be received by the offspring, whereas the offspring optimum determines the upper bound of PI. The zone between these two optima has been called the 'battleground' on which POC will be played out (Godfray 1995a). The width of the battleground depends primarily on the degree of relatedness within and between broods, asymmetries in the reproductive values of offspring, and whether care is provided by one or both parents (Parker 1985; Godfray 1995a; Mock & Parker 1997, 1998; Parker et al. 2002; Fig. 1a).

What is the equivalent battleground in reproductive skew (RS) theory? Most skew models examine conflict between a dominant and a subordinate over shares of the total reproductive output of the group. Unlike POC models which assume diminishing returns on increasing PI, the 'classical' skew models of Vehrencamp (1979, 1983) and Reeve et al. (Reeve 1991; Reeve & Ratnieks 1993) are zero-sum, so that any loss to the dominant represents an equivalent gain to a subordinate. The assumption is that there is a constant linear relation between an individual's reproductive share and its direct fitness. When fitness returns are linear in this way neither individual gains from sharing with the other; that is, the battleground is simply all of the available reproduction. Crucially, however, classical skew models include a layer of constraints that are absent from POC theory: subordinates may leave the group, or be evicted. (Offspring, by contrast, usually cannot leave the nest to seek PI elsewhere.) These options outside the group place constraints on the share of reproduction that can be claimed by both dominants and subordinates. If dominants are free to choose their own share of reproduction, they can sometimes gain by offering a 'staying incentive' for the subordinate to remain if this boosts productivity (Vehrencamp 1979, 1983; Emlen 1982; Reeve 1991). Conversely, if subordinates can choose their own level of reproduction, they should claim up to the dominant's 'eviction threshold', that is, the share beyond which a dominant does best to evict the subordinate from the group (Johnstone & Cant 1999a). Thus, the 'staying incentive' places a lower bound on the reproductive share that a subordinate in a stable group must receive, while the 'eviction threshold' places an upper bound on the share that a subordinate can safely claim. These 'group stability constraints' define the battleground (or 'window of selfishness'; Reeve & Keller 1997) of classical RS theory (Fig. 1b). The width of the battleground depends on three factors: relatedness, ecological constraints on dispersal, and the productivity benefit of retaining a subordinate.

Thus, the nature of the constraints or bounds defining the battleground is different in POC versus RS theory, but it is important to remember that this is not a natural distinction. Rather, it arises simply because the shape of the assumed benefit function or 'utility curve' is different in the two modelling frameworks. Skew theory is framed by group stability rather than by optimization constraints because of the assumption of linear fitness returns with increasing reproductive share. If, as might be more realistic, we assume diminishing returns with increasing reproductive share, dominants and subordinates may do best to take some intermediate optimum share of the available reproduction (see Appendix). These optima for the dominant and subordinate will act as a second layer of constraints to overlay those concerned with group stability, and these 'optimization' constraints can render the original bounds irrelevant (as I show in the Appendix). For example, in vertebrates, where there are often strict physical or physiological constraints on the number of eggs that can be laid, or the number of fetuses that can be gestated, group stability constraints may play little role in defining the battleground (Cant & Johnstone 1999).

How can we identify which bounds apply in nature? One method of testing whether group stability constraints are important would be to manipulate these constraints and look for an effect on skew. For example, one could create or remove external breeding opportunities for subordinates and look for the predicted effect on their reproductive share. Conversely, one could manipulate skew and look for an effect on group stability. Indeed, this latter type of experiment has already been performed, albeit with a different objective in mind. Experiments in which subordinate males are denied access to females during the fertile period have been conducted several times in cooperatively breeding birds to test the relation between paternal care and paternity (reviewed in Wright 1998). These experiments have never led to the dissolution of the group, as one would expect if the battleground was defined primarily by group stability constraints. In fact, there is currently very little evidence in any species to support the idea that group stability constraints determine the battleground over reproduction. This is important because until we know the defining limits of the

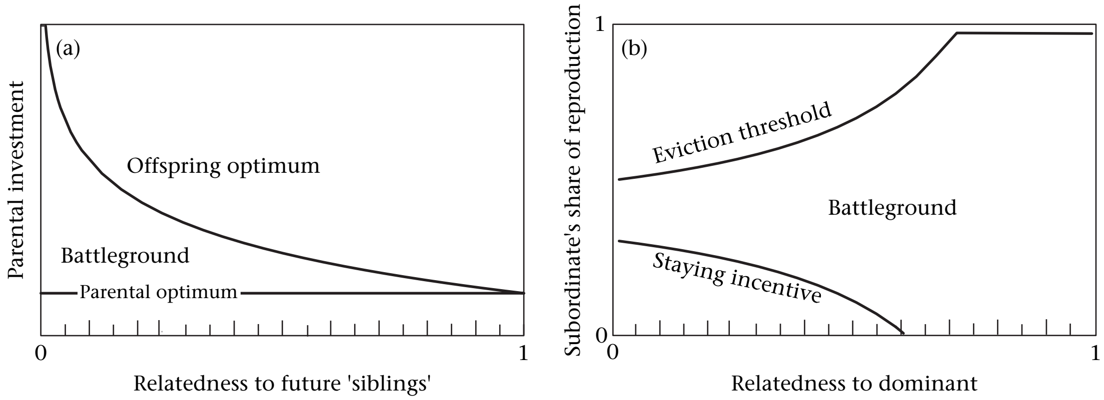

Figure 1. Defining limits of the battleground in parent–offspring conflict (POC) and reproductive skew theory. (a) The upper and lower bounds of the POC battleground are set by the optimum level of parental investment from the perspectives of the offspring and the parent, respectively. Parents are assumed to be equally related to current and future offspring, and so should allocate the same optimal level of parental investment to each (the 'parental optimum'). From the perspective of an individual offspring, however, the optimum level of PI declines as its relatedness to the future offspring of the parent ('siblings') increases, until the optima for parents and offspring coincide at $r = 1$. (b) In reproductive skew theory, the limits of the battleground are set by the requirement for group stability. The lower bound or 'staying incentive' is the minimum fraction of reproduction that the subordinate requires to make staying in the group worthwhile; the upper bound or 'eviction threshold' is the maximum share that the subordinate can claim before it pays the dominant to evict it. Stable groups can form in the region between these bounds.

battleground it is difficult to understand how conflict within it will be resolved.

MODELS OF CONFLICT RESOLUTION

Given the potential genetic conflict between parents and offspring, or between dominants and subordinates, how are we to predict the outcome of evolution? For POC, 'parent wins' is usually viewed as the default outcome because of the overwhelming physical dominance of parents over offspring: as Trivers (1974) remarked, a calf cannot fling its mother to the ground to suckle from her at will. However, offspring may adopt more subtle means to extract greater PI from parents than parents are selected to give. For example, Zahavi (1977) suggested that offspring could 'blackmail' parents into providing them with greater investment through costly solicitation or begging behaviour. This idea was first modelled by Parker & Macnair (1979) who showed that costly begging could indeed result in a 'compromise' evolutionarily stable strategy (ESS) in which the level of investment in young was intermediate between the optima of parents and young. But why should not parents evolve to ignore the solicitations of their offspring? This possibility did not enter into the model of Parker & Macnair (1979), in which the parental response to begging was an assumption of the model rather than an evolved strategy. Eshel & Feldman (1991), however, showed that conditions can indeed exist where offspring are selected to engage in costly begging and parents are selected to respond with increased investment. This is because costly begging, while depressing offspring survival for a fixed level of investment, can increase the slope of the offspring utility curve so that the parent's optimum PI is shifted to a new, higher level of investment. In some circumstances, this increased investment is more than enough to compensate the offspring for the costs of solicitation. In effect, an offspring can handicap itself in such a way that parents are selected to overcompensate. The important take-home message from these resolution models is that, even in the face of overwhelming physical superiority, a weaker party may win out by wielding more subtle weapons of control, such as costly displays.

In the context of skew theory, the original 'optimal' skew models of Vehrencamp (1979, 1983) and Reeve (1991) assumed that 'dominant wins' was the only possible outcome of natural selection. That is, socially dominant individuals were assumed to have complete control over reproductive shares, pushing the level of subordinate reproduction down to the lower bound determined by constraints on group stability. As we have learned from POC, however, the intuitive nature of such solutions can be misleading. If 'compromise' (and even 'offspring wins'; Parker & Macnair 1979) solutions are possible when a parent competes with its offspring, then clearly the assumption of 'dominant always wins' among competing adults is open to question on theoretical (in addition to empirical) grounds. Nevertheless, it is true that dominants are usually older, larger or in some way physically superior to subordinates, so it seems reasonable to accept that 'dominant wins' will be the default solution unless subordinates have some way of manipulating reproductive shares.

So far there have been two skew models that allow subordinates a degree of control over reproductive shares within the battleground of conflict, and which therefore result in a 'compromise' between the interests of dominant and subordinates. Perhaps the simplest way for subordinates to claim a share of reproduction, if they can get away with it, is to add young to the dominant's brood. Cant (1998) analysed a sequential game in which first a dominant and then a subordinate female contributed eggs to a communal clutch. Related subordinates are selected to add fewer eggs because of the negative impact this has on the dominant's reproductive success. Effectively, the game takes place in a battleground defined by optimization constraints, and group stability constraints play no role. The model has subsequently been extended to incorporate the possibility of indiscriminate (Johnstone & Cant 1999b) and discriminate (Hager & Johnstone 2004) infanticide. These models have the advantage that the mechanism by which effort (number of eggs or degree of infanticide) translates into reproductive success (number of surviving young) is made explicit, providing clear opportunities to test the predictions against nature.

A second resolution model, this time operating within the battleground defined by group stability constraints, is provided by Johnstone (2000; building on an original model by Reeve et al. 1998). Here, dominant and subordinate engage in a 'tug of war' over disputed reproduction between the upper and lower bounds of subordinate shares. The disputed share is partitioned according to the level of effort each party puts into the tug of war, with dominants being awarded an efficiency advantage in their 'tug', but the total amount of reproduction available to be shared decreases with the total effort expended in competition. This is because time and effort expended on reproductive conflict could otherwise be spent in cooperative activities. The outcome in this model is necessarily a compromise between the interests of the two parties, depending on their relative strength. While providing a broad framework for understanding the outcome of conflict in cooperative groups, the very generality of the tug-of-war model makes it rather difficult to test. What exactly is meant by 'selfish effort', and how will it be manifested? Does the nature of the selfish effort matter for the outcome of the model?

SOCIAL AGGRESSION AND SKEW

Clearly there is scope for further theoretical work on the resolution of conflict over reproduction. We require models that make explicit the manner in which one individual can control the reproductive share of another. That is, we require models that specify the means that an animal might use to exert a 'tug' in a tug of war. One promising area that has been largely neglected is to explore how direct aggression could be used to resist suppression. This has far-reaching consequences because even more subtle forms of control, such as the use of inhibitory pheromones, must ultimately be backed up by force to be evolutionarily stable (Keller & Nonacs 1993).

Aggression as a means of evading suppression was first put forward in an early skew model. Reeve & Ratnieks (1993) considered a case where dominants must offer a fraction of reproduction as a 'peace incentive' to deter subordinates from engaging in a lethal fight for control of the nest. This model treated aggression as an escalated, all-or-nothing event leading to the death of the loser. Most of the observed aggression in animal societies, however, is of a milder, nonlethal form. Such interactions may represent attempts by dominants and subordinates to increase the marginal cost to their opponent of attempting to monopolize reproduction, rather than the precursor to an all-or-nothing fight for control of the nest. Of course, where the benefits of increasing reproduction are linear the value of a share p to dominants and subordinates is equal, that is, the subordinate's gain is exactly the dominant's loss. If the costs of fighting are lower for dominants then subordinates are doomed to lose out. Given diminishing returns, however, subordinates stand to gain much more from a small increase in their reproductive share than dominants stand to lose. In these circumstances, aggression may be an effective method of resisting suppression, even if the costs of a fight weigh more heavily on the subordinate. That is, dominants may do better to concede a small and (for them) cheap share of reproduction rather than enter into an escalated contest with a highly motivated subordinate (Reeve & Keller 1997).

A key determinant of the efficacy of aggression as a means of evading suppression will be the way in which the marginal costs of aggressive acts are distributed between actor and recipient. Who pays the cost of an aggressive act? One can imagine a continuum between 'displays', which are costly to the aggressor, and 'blows', the costs of which are borne by the recipient of aggression. A second axis arises if aggression entails costs to group productivity, as it does in the tug-of-war model of Reeve et al. (1998). The different forms of cost have been a central focus of POC models, but they remain largely unexplored in models of RS. For example, begging models have examined the resolution of sibling competition where (1) the costs of displays are borne individually, (2) they are a function of the average begging level in the nest, and (3) they scale with summed levels of displays (Parker 1985; Mock & Parker 1997). A similarly detailed treatment of the variety of costs in models of reproductive conflict would help us to understand social power and the ways in which animals might resist it, and shed light on patterns of variation between individuals, and between groups, in the level of aggression.

TESTING THE THEORIES

Despite their similarities of structure, the approach to testing the two theories has been very different. Empirical tests of POC theory typically focus on overt behavioural signs of the underlying evolutionary conflict, for example, infanticide, siblicide or costly begging behaviour (reviewed in Mock & Parker 1997; Wright & Leonard 2002). However, Mock et al. (Mock & Forbes 1992; Mock & Parker 1997) warned against using observations of overt conflict (which they term 'squabbling') as prima facie evidence in support of the theory. This is because such squabbles may occur for reasons other than the genetic (or, strictly, reproductive value) asymmetries identified by Trivers (1974), for example, as part of an honest signal of need by offspring to parents (Godfray 1991, 1995b; Godfray & Johnstone 2000). Nevertheless, if there were no misalignment of interests between parents and offspring, it is difficult to see why signals between them should take the form of costly displays rather than 'conspiratorial whispers' (Krebs & Dawkins 1984). Offspring would not be forced to engage in costly signalling to establish credibility because there would be no incentive for deception. Costly signals (over and above the minimum level required for signal detection) do, therefore, imply an evolutionary conflict of interest between family members at some level.

While evolutionary conflict may exist, however, it is not necessarily selectively important. For POC theory to have heuristic value it should be demonstrated that observed phenotypes have been moulded by the conflict of interest between parents and young, rather than by selective pressures unrelated to this particular social interaction. This is a more challenging objective. Mock & Parker (1997) argued that the best tests of POC will be those that can demonstrate (1) that parents and offspring act as if at cross purposes (i.e. there are signs of overt conflict), (2) that when parents are allowed to 'win', offspring fitness is measurably reduced, and, conversely (3) that when offspring are allowed to 'win', parental fitness suffers measurably.

A similar set of criteria could usefully guide attempts to test RS theory. Experimental manipulation of reproductive shares (equivalent to allowing a dominant, or a subordinate, to 'win') would be informative in three ways. First, such manipulations could be used to measure just how costly, if at all, subordinate reproduction is to the reproductive success of dominants. Second, the effect of a manipulation of skew on group dynamics and productivity would help to determine which type of constraints, group stability or optimization, define the zone of conflict. For example, if manipulations do not lead to the dissolution of the group, then it is likely that the battleground is defined by optimization rather than group stability constraints, and the zone of conflict will depend (as it does in POC theory) primarily on the level of relatedness between group members rather than external ecological constraints. Third, the behavioural response of dominants and subordinates to a manipulation of skew would shed light on the mechanisms by which conflict is resolved, for example through aggression or the withdrawal of cooperation. Such experiments would be more useful than the usual approach to testing RS theory via its 'boundary predictions'. This involves making an assumption about which party, dominant or subordinate, has control over reproductive allocations, and then comparing the predictions associated with that boundary of the battleground with correlational data across groups or species (e.g. Reeve et al. 1998; Reeve & Keller 2001). This sort of evidence is equivocal because different models make similar correlational predictions (e.g. Reeve 1991; Cant 1998; Johnstone 2000), and there is usually little information about which party controls reproduction.

The best attempt to date to distinguish rival skew models also illustrates the difficulties in doing so via their correlational predictions. Langer et al. (2004) performed an elegant experiment in which they created 'designer groups' of high and low relatedness in the social bee *Exoneura nigrescens*, and varied ecological constraints on dispersal in experimental plots. They found that high-relatedness groups shared reproduction more evenly and were more productive than low-relatedness groups, and that variation in ecological constraints had no effect on skew. These findings are strong evidence against the concession model of skew as they suggest that group stability constraints have no impact on the division of reproduction in this species. More debatable, however, is the authors' interpretation of their results as providing good support for the tug-of-war model. This is because (1) the effect of relatedness is predicted to be weak or nonexistent in the tug-of-war model (Reeve et al. 1998), (2) other skew models also predict greater sharing of reproduction and greater productivity between relatives (e.g. Appendix; Cant & Johnstone 1999), and (3) the result that groups of high relatedness are more productive is consistent with models of helping effort based on kin selection (Cant & Field 2001, 2005; Kokko et al. 2001). Langer et al.'s study provides a convincing falsification of concession models, but rigorous testing of the tug-of-war model is difficult because of the nondiscriminating nature of its predictions.

An alternative tactic for studies of reproductive skew is to shift focus from the question of who wins, and what shares are thereby obtained, to examine overt signs of underlying conflict, such as social aggression. It is sometimes argued in RS theory that the width of the battleground (or 'window of selfishness') should be correlated with the level of aggression (Reeve & Keller 1997; Reeve 2000). The reasoning is that where the optima of two parties are most divergent there is greater scope for overt conflict, since in these circumstances the consequences of victory for one or the other party are more starkly differentiated. In general, however, it is not this difference in outcome that will be the prime determinant of the level of behavioural conflict, but rather the costs and benefits to each party of engaging in, or escalating their level of, aggression. Two individuals may have widely different interests, but if aggression carries a severe risk of death or injury then overt conflict may be rare and the combatants may choose to resolve the conflict peaceably. Conversely, where aggression carries little risk of injury or death, overt conflict may be common even when there is little to squabble over. (One is reminded of Henry Kissinger's remark about university politics: disputes are so vicious because the stakes are so low.) More formally, if the fitness of two individuals w_1 and w_2 is a function of their own aggression level a and that of their partner, the ESS levels of aggression will be determined by the slopes $\partial w_1(a_1, a_2)/\partial a_1$ and $\partial w_2(a_1, a_2)/\partial a_2$, not the width of their zone of conflict. To illustrate, the battleground of reproductive skew theory is at its widest when relatedness equals 1, yet under these circumstances dominant and subordinate should be neutral as to the division of reproduction, and so have nothing to gain from aggressive acts (Cant & Johnstone 2000).

The question of how underlying genetic conflict is manifested in overt actions is fundamental to our understanding of patterns of social behaviour. As described, social aggression may plausibly represent the direct exercise of power or control over reproductive shares. Parent–offspring conflict theory, however, suggests alternative, more subtle roles for aggression in animal societies. For example, aggression by subordinates may parallel the begging behaviour of offspring as a competitive display or an honest signal of need. That is, subordinate aggression may be a way of manipulating dominants into giving up reproduction by inflicting costs on themselves, on a dominant or on the group (in a manner analogous to scramble models of begging; Parker & Macnair 1979; Parker 2002), or it may convey information as to what share of reproduction a subordinate 'requires' to stay in the group or refrain from challenging the dominant's status (analogous to signalling models of begging; Godfray 1991, 1995b; Godfray & Johnstone 2000). Subordinates may aggressively 'test' dominants to determine their relative strength or quality (Reeve & Ratnieks 1993; Cant & Johnstone 2000). The displays of dominants, for their part, may act as a deterrent signal to discourage subordinates from engaging in an escalated contest. Animal conflict has been the focus of evolutionary game theory since its inception (Maynard Smith & Price 1973), but we have surprisingly little theory to help understand the function and consequences of aggression in cooperative societies (Clutton-Brock & Parker 1995; Frank 1995; Reeve & Nonacs 1997; Reeve et al. 1998; Cant & Johnstone 2000; Reeve 2000). Models that make specific assumptions about the function of aggression offer opportunities to test between the candidate hypotheses. This area of research is in its infancy.

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Appendix: Diminishing Returns and Reproductive Skew

Classical reproductive skew theory (Vehrencamp 1979, 1983; Reeve 1991) assumes that fitness is an increasing linear function of reproductive share. This contrasts with the standard assumption of POC theory (and, indeed, life history theory in general) that increasing consumption or utilization of a resource will bring diminishing returns in terms of individual fitness (Trivers 1972, 1974; Parker et al. 1989). A law of diminishing returns will also apply to reproductive shares whenever there are accelerating costs associated with producing young, so that each successive offspring is more expensive to produce than the last. This may occur, for example, when there are limiting resources for offspring production, or physical constraints on the number of young that can be gestated or incubated. Here, I show that incorporating the law of diminishing returns into classical skew models can render their original predictions irrelevant, and provide a simple alternative explanation for patterns of reproductive sharing.

Assume that groups consist of a single dominant individual, who controls reproductive shares, and n subordinates. Let the net direct fitness of the dominant increase with its fraction q of reproduction according to the function $G(q)$ (where $G'(q) > 0$). Any fraction p $(=1-q)$ of reproduction not monopolized by the dominant can be shared with n related individuals of relatedness coefficient r. For simplicity, assume that these other individuals compete in a scramble for the remainder of the resource so that, on average, each obtains a share p/n. The model could easily be adapted to analyse other possibilities; for example, Parker et al. (1989) modelled evolutionarily stable patterns of food sharing between chicks when control of a resource passes sequentially from stronger to weaker individuals. The same approach could be used here to examine patterns of reproductive skew in societies where control over reproduction passes from one individual to another down a dominance hierarchy.

Given the above assumptions, the inclusive fitness of the dominant, W_d, can be written

$$W_\mathrm{d} = G(q) + rnG((1-q)/n) \tag{1}$$

When will the dominant do best to share reproduction? The optimum share q^* for the dominant is that which satisfies $W'_\mathrm{d} = 0$ (where a prime denotes the derivative with respect to p). Differentiating equation (1) with respect to q and setting it equal to zero we have

$$G'(q) - rG'((1-q)/n) = 0$$

from which it can be deduced that $q^* < 1$ where

$$rG'((1-q)/n) > G'(q) \lim p \to 1 \tag{2}$$

(see also Fig. A1).

Since $r < 1$, this inequality implies that sharing can be favoured only when the initial slope of the gain curve is greater than its final slope (given $G'(q) > 0$). In other words, a diminishing returns fitness function ($G''(q) < 0$) is a necessary condition for resource sharing to be favoured by kin selection. Inequality (2) further implies that the owner will not share the resource unless $r > 0$, regardless of the shape of $G(q)$, and that the greater the difference between the initial and final slopes of the gain curve (i.e. the more rapidly the marginal benefits decrease with increasing reproductive share), the lower the

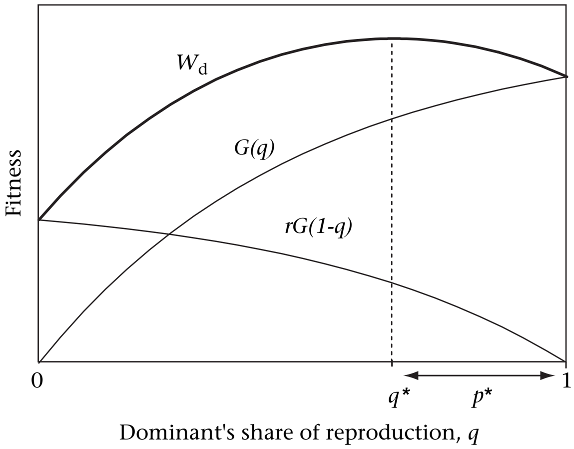

Figure A1. Optimal reproductive sharing between two individuals under diminishing returns. The direct fitness of a dominant individual increases with its reproductive share q according to the function $G(q)$. The indirect fitness payoff to the dominant of allocating a share $p = 1 - q$ to a related subordinate is given by the function $rG(1 - q)$. The dominant's inclusive fitness payoff $W_{\rm d}$ is the sum of these two curves, and is maximized at $q^* = (1 - p^*)$. The allocation of p^* to the subordinate is referred to as the optimal level of 'beneficial sharing'.

threshold value of relatedness above which reproductive sharing is favoured. Finally, the constraint that $r < 1$ means that the optimum dominant's share, q^*, must be greater than $1/(n + 1)$. This is because q^* satisfies $G'(q^*) = rG'(p^*/n)$, which, given the requirement of diminishing returns can hold only where $q^* > p^*/n$, i.e. $q^* > 1/(n + 1)$. In other words, the model predicts that the dominant will always receive the larger share of reproduction.

How does this analysis compare with that of classical skew models? Consider a dominant and a single subordinate. Let the level of p that maximizes the dominant's inclusive fitness be denoted p^*. This share will be referred to as the optimal level of 'beneficial sharing' to distinguish it from the staying incentive in classical skew theory. As described, p^* satisfies $\partial W_{\rm d}'/\partial p = 0$ at $p = p^*$. Let the minimum staying incentive required to retain the subordinate in the group be denoted by $p_{\rm s}$. This staying incentive satisfies

$$kG(p_{\rm s}) + rkG(1 - p_{\rm s}) = x + r$$

where k is the ratio of productivity of a two-player group compared to that of a lone breeder, and x is the probability that the subordinate disperses successfully. The left-hand side of the above equation represents the inclusive fitness payoff to the subordinate if it stays in the group and the right-hand side its payoff if it departs (this formulation assumes $G(1) = 1$, i.e. the payoff to a lone breeder equals 1). If $p^* = p_{\rm s}$, then group stability constraints are irrelevant: the subordinate will receive p^* regardless of the level of ecological constraints. Just how 'bowed' must the curve $G(p)$ be for $p^* > p_{\rm s}$? Figure A2 shows two example gain curves that vary in the rate at which the marginal benefit of increasing reproductive share declines, and the corresponding values of p^* and $p_{\rm s}$ as a function of relatedness. Above some critical level of relatedness p^* exceeds $p_{\rm s}$ (thus rendering the staying incentive irrelevant). The more 'bowed' the diminishing returns curve, the lower the critical level of relatedness above which $p^* > p_{\rm s}$. We could similarly plot the optimal level of beneficial sharing assuming that the subordinate controls reproductive shares (which, ceteris paribus, is equal to $1 - p^*$), and compare this against the eviction threshold in classical skew theory (Johnstone & Cant 1999a; Johnstone 2000). Again the prediction is that group stability constraints are more likely to be rendered irrelevant at higher levels of relatedness.

Determining whether group stability constraints are relevant is important for skew theory because the relation between p^* and, say, relatedness r is different from the relation between $p_{\rm s}$ and r. Specifically, classical skew models predict that $\partial p_{\rm s}/\partial r < 0$, so that a subordinate's reproductive share decreases with relatedness (Vehrencamp 1983; Reeve 1991). In the beneficial-sharing model, by contrast, $\partial p^*/\partial r > 0$, i.e. a subordinate's share increases with relatedness. This is the same effect as that seen in the 'costly young' skew model of Cant & Johnstone (1999), where the

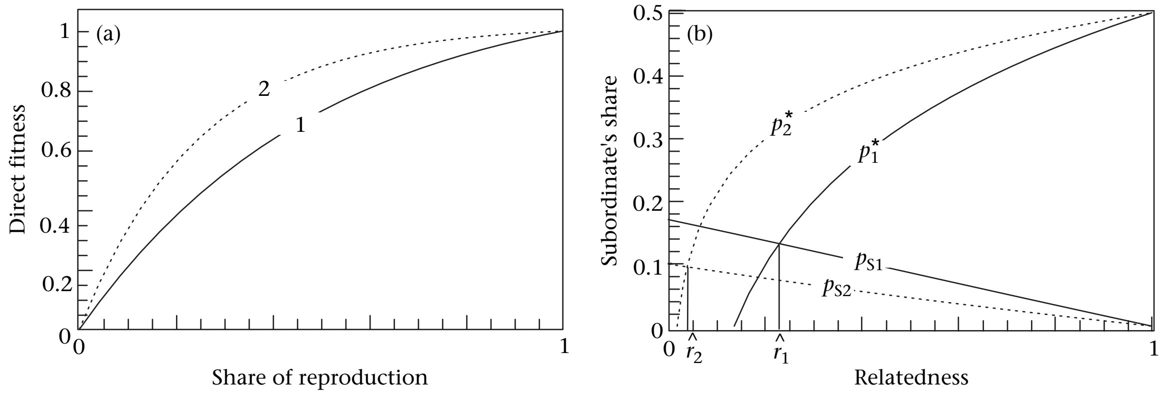

Figure A2. Comparing the optimal level of beneficial sharing p^* and the staying incentive $p_{\rm s}$. (a) Two illustrative curves showing diminishing returns. The curves are generated from the function $(1 - e^{-zp})/(1 - e^{-z})$ where the parameter z controls how 'bowed' the diminishing returns curve is with (1) $z = 2$ and (2) $z = 4$. (b) The corresponding level of 'beneficial sharing' (p^*) and staying incentive ($p_{\rm s}$). Above a critical level of relatedness $\hat{r}$, the optimal level of beneficial sharing exceeds the staying incentive and the original group stability constraints of classical skew models are rendered irrelevant.

assumption of accelerating costs of producing young is equivalent to assuming diminishing net fitness returns with increasing reproductive share. Thus, the current model predicts that groups of close relatives will share reproduction more evenly, and will be more productive than unrelated groups, matching the recent results of Langer et al. (2004) on a social bee *E. nigrescens*.

It was Hamilton (1964) who originally recognized that a dominant chick will share PI with a full sibling when the next unit of PI is more than twice as beneficial to the subordinate chick's fitness as to its own. Substitute the word 'breeder' for 'chick', and 'reproduction' for 'PI', and you have the beneficial-sharing model. Diminishing returns curves are a standard feature of evolutionary models in all aspects of life history; their absence from skew theory is unfortunate because it has led to the most simple explanation for reproductive sharing being overlooked.