

A skew model for the evolution of sociality via manipulation: why it is better to be feared than loved

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Concession-based reproductive skew models predict that social groups can form via persuasion, whereby dominant individuals forfeit some reproduction to subordinates as an incentive to stay and help. We have developed an alternative skew model based on manipulation, whereby dominant individuals coerce subordinates into staying and helping by imposing costs on their independent reproductive prospects. Stable groups can evolve under a much wider range of genetic and ecological conditions under this manipulation model than under concession models. We describe evidence that various forms of preemptive and ongoing manipulation occur in nature and we discuss the implications of the model for the development of a general theory of social evolution.

Keywords: reproductive skew model; social behaviour; cooperation; manipulation

‘From this arises a debate: if it is better to be loved than to be feared, or the contrary. I reply that it would be nice to be both, but because they are difficult to combine together, if you cannot have both, it is much more secure to be feared than to be loved’

Niccolò Machiavelli (1532)

1. INTRODUCTION

One approach to understanding the evolution of social behaviour involves the development of models which integrate inclusive fitness effects, ecological constraints on independent breeding and mutualistic group benefits into a predictive framework. The first such models were developed by Emlen (1982) and Vehrencamp (1983*a,b*). Vehrencamp’s (1983*a,b*) model assumed that social groups were comprised of a dominant individual and a subordinate, that the dominant controlled reproduction of the subordinate and that the subordinate had two options, i.e. staying and helping or leaving and attempting to breed independently. Based on these assumptions, the model predicted under what circumstances with regard to relatedness level, degree of ecological constraint and magnitude of mutualistic benefit a social group should form and how groups should differ in their distribution of reproduction among individuals (reproductive ‘skew’).

One of the most important and novel predictions of reproductive skew theory is that a dominant individual should, in certain situations, yield reproductive concessions to the subordinate as an incentive for the subordinate to stay and help rather than leave (see also Alexander (1974), pp. 350–351). Similarly, Reeve & Ratnieks (1993) showed that dominants might also concede some reproduction to subordinates to dissuade them from engaging the dominant in a fight (see also Reeve & Keller 1997). Reproductive skew models thus entail a form of ‘social contract’ between dominants and

subordinates, whereby the subordinate agrees to stay and help in exchange for a share of the group reproduction.

Tests of reproductive skew theory have focused on (i) analysis of its critical assumption of dominant control over subordinate reproduction (Clutton-Brock 1998), (ii) detection of a social contract via experimental violation of a presumed agreement (Reeve & Nonacs 1992, 1993; Strassmann 1993), and (iii) comparison between the observed and predicted patterns of covariation between relatedness, the degree of ecological constraint, and the magnitude of skew, both within species (Field *et al.* 1998) and among taxa (Bourke & Heinze 1994; Heinze 1995; Reeve & Keller 1995; Emlen 1996; Crespi & Choe 1997; Jamieson 1997). As yet, we have no clear evidence for either complete control by dominants or the presence of social contracts, and the empirical evidence is either broadly but weakly consistent with the predictions of the theory (see the review in Keller & Reeve (1994)) or opposed to them (Field *et al.* 1998).

The lack of consistent support for the assumptions and predictions of the original ‘optimal skew’ models promulgated by Vehrencamp (1983*a,b*) and Reeve & Ratnieks (1993) has motivated the development of models with different assumptions and an expanded range of behavioural options for dominants and subordinates. The expanded range of assumptions includes situations with (i) incomplete control of subordinates by dominants (Reeve *et al.* 1998), (ii) variable brood sizes and costs of reproduction for dominants (Cant 1998; Cant & Johnstone 1999), or (iii) multiple subordinates (Johnstone *et al.* 1999), and the range of behavioural options now allows for (i) inheritance by subordinates (Kokko & Johnstone 1999; Ragsdale 1999), or (ii) eviction of subordinates by dominants (Johnstone & Cant 1999). Most of these models yield predictions which differ considerably from those of the original skew models and, in some cases, their predictions accord well with data from natural populations of social animals (e.g. Ragsdale

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1999). The success of some of these models indicates that to develop general theory for the evolution of sociality we must formulate a range of related models, each of which applies to taxa exhibiting different behavioural repertoires (Clutton-Brock 1998; Johnstone & Cant 1999).

We believe that, for most social animals, reproductive concessions are unrealistic and most cooperative interactions are based instead on the direct adjustment of subordinates' behaviour by dominant individuals. In this paper we present a model for the evolution of social behaviour which is based on one type of behavioural adjustment, i.e. manipulation. We assume that dominants impose costs on subordinates which tip the behavioural decisions of subordinates towards staying and helping rather than leaving. Thus, rather than providing reproductive benefits (concessions) to subordinates in order to induce them to stay and help, dominants impose costs on subordinates which make staying and helping the subordinate's best strategy. Our model was inspired by Alexander's (1974) 'parental manipulation' concept and it includes the same key variables, i.e. relatedness, ecological constraints and mutualistic benefits, as previous skew models. We describe our model, discuss how well its assumptions and predictions are satisfied and focus on how these predictions contrast with those of concession-based models.

2. MODEL

Reeve & Ratnieks (1993) inspected the conditions favouring the formation of social groups and the extent to which reproduction is shared given the degree of ecological constraints (x), cooperative benefits (k) and relatedness (r) of group members. They assumed that the cooperative benefits exceed the reproductive output of an already established solitary breeder ($k > 1$) and that the dominant controls subordinate reproduction. When subordinates are selected to disperse, but dominants gain from subordinate retention (i.e. $xr < k - 1 < x/r$), they determine the conditions under which the dominant will concede some reproduction to the subordinate as a 'staying incentive'. We use this theoretical set-up to ask instead, when should the dominant administer a cost on subordinate independent reproduction to 'manipulate' it into staying? We do not assume that the dominant controls subordinate reproduction, but we do assume complete skew (i.e. that the dominant monopolizes reproduction) and, given this, we assume that relatedness is greater than zero (providing the subordinate with some fitness incentive to join the dominant).

Manipulation, which is defined as the cost the dominant imposes on the subordinate's independent breeding prospects (m), could reduce the fitness of the dominant by causing the subordinate to be a weaker helper. To account for this possibility, we define c as the 'coefficient of helping impairment', which represents the slope of the relationship between the amount of harm which returns to the dominant (via obtaining a weaker helper) per unit cost absorbed by the subordinate (m). Given that a dominant might hurt its own potential helper, it is still favoured to manipulate when

$$k - 1 - cm > xr_{ds}, \quad (1)$$

where r_{ds} denotes the relationship between the relatedness of the dominant to its own offspring relative to its relatedness to the subordinate's offspring (Reeve & Keller 1995). Translating equation (1) into words, we show that the dominant will manipulate when the benefits of cooperation are high enough to buffer the cost of retaining a poorer helper (relative to an unmanipulated helper).

If equation (1) is met, we assume that the subordinate cannot escape the costs of manipulation to itself and it should join the dominant when

$$r_{sd}(k - 1 - cm) > x - m, \quad (2)$$

where r_{sd} is the relatedness of a subordinate to its own offspring relative to its relatedness to the dominant's offspring (Reeve & Keller 1995). Equation (2) simply demonstrates that a subordinate will remain when its reproductive prospects drop below its expected fitness from staying and helping.

By rearranging equations (1) and (2) and solving for m , we determine that social groups will evolve via manipulation when

$$k - 1 > x[r_{ds} + c(1 - r_{sd}r_{ds})]. \quad (3)$$

Inspection of equation (3) reveals three noteworthy predictions. First, if manipulation does not impede the subordinate's ability to help ($c = 0$) then there is no theoretical limit on the extent of manipulation—thus manipulation will occur whenever the dominant derives a net benefit from retaining a subordinate. Intuitively, the more that manipulation damages the subordinate's helping ability relative to obstructing its independent breeding (increasing c), the greater the cooperative benefits (k) must be to absorb this loss of helper efficiency and to favour group formation. Second, as expected, social groups will form most readily when the relatedness is asymmetrical (when the subordinate is more closely related to the dominant's offspring than is the dominant to the subordinate's offspring). This result agrees with previous work on parental manipulation (e.g. Charnov 1978). In addition, low relatedness increases the range of skew parameter values under which social groups will emerge via manipulation. Third, because it is easiest to manipulate subordinates with relatively low breeding expectations into staying and because the dominant loses relatively less indirect fitness by manipulating subordinates with lower expected breeding success, dominants will prefer to manipulate offspring (or entire clutches) with relatively low dispersal and breeding opportunities. We note, however, that subordinates with particularly low expected breeding opportunities are expected to stay and help voluntarily, such that coercion is unnecessary (see Brown & Pimm (1985) and Marzluff *et al.* (1996) on low-quality males in scrub-jays).

Some forms of manipulation, such as reducing the feeding levels or rates of developing young, are cheap and easy for the dominant to perform, whereas other forms, such as harassment or disruption of breeding attempts, will demand some energy or time investment by the dominant. We incorporate these potential direct costs of manipulation to dominants into the model by defining d as 'the coefficient of manipulation investment', where d is the slope of the relationship between the cost the

dominant pays to manipulate relative to the amount of damage it causes. Repeating the same steps from above, substituting d for c , we find that stable associations will result when

$$k - 1 > x(r_{ds} + d)/(1 + dr_{sd}). \quad (4)$$

Equation (4) produces the same qualitative patterns as equation (3) regarding the influence of productivity benefits, ecological constraints and relatedness on the formation of social groups. However, we find that subordinates are less willing to join dominants when their helping ability is compromised than when dominants incur a direct cost of manipulation.

How do the predictions of our model compare with those of concession models? Reeve & Ratnieks (1993) determined that a dominant will forfeit some of its direct reproduction to induce a subordinate to stay (by altering the relative prospects of dispersal) when $k - 1 > x$. The result is a stable association with shared reproduction. Our model generates the same conditions (under some parameter values) for the formation of social groups arising from manipulation (where the relative pay-offs of dispersal are also altered). However, our model produces fundamental differences. First, the conditions favouring sociality arising from manipulation are much more lenient than those originating from concessions: we generate $k - 1 > x$ only under the extreme values of $d = 1$ or when both $c = 1$ and $r_{sd} = 1$ (figure 1). Provided that $d < 1$ or $c < (1 - r_{ds})/(1 - r_{sd}r_{ds})$ social groups arising via manipulation can evolve where concession-based groups will not evolve.

Our model also demonstrates that, if groups have evolved via manipulation, then the predictive power of Reeve & Ratnieks' (1993) concession-based model is completely lost. This is because their model predicts shared reproduction (the degree of skew being determined by x , r and k) when $k - 1 > x$, but our model allows for complete skew under exactly the same conditions (figure 1). However, Reeve & Keller (1995) predicted stable complete skew when $k - 1 > x$ if the subordinate is genetically indifferent between rearing full siblings or its own offspring ($r_{sd} = 1$). We too generate this prediction if the subordinate's helping ability is maximally compromised ($c = 1$). However, again, if the subordinate's helping ability does not proportionately decrease with dispersal ability ($c < 1$) our model allows the formation of social groups under lower values of cooperative benefits (figure 1).

3. DISCUSSION

To the best of our knowledge, our model is the first to consider manipulation in the skew model framework. The main finding from the model is that the ecological and genetic conditions for the evolution of stable cooperative associations are considerably less restrictive under manipulation than under concessions. In particular, our model implies that it is much easier for social groups arising from manipulation to evolve (and express complete reproductive skew) than for groups arising from reproductive concession to evolve (and display the same or lower levels of reproductive skew). The explanation for this is simple:

when reproduction is conceded, the dominant's loss is directly proportional to the subordinate's gain, but when dominants manipulate, they may lose proportionately less to retain the subordinate. It does not matter whether a dominant hurts a subordinate's dispersal prospects or enhances its staying prospects; a subordinate will opt to stay as long as it is its best available strategy.

The usefulness of our model as an alternative to concession-based theory depends upon the presence and extent of manipulation in nature. Manipulation can take a multitude of forms, all of which engender a dominant individual reducing a subordinate's prospects for leaving and breeding independently. Prior to reproductive maturity, mothers or other dominant individuals may manipulate by leaving material out of eggs or young (e.g. Fukatsu & Ishikawa 1992), feeding an offspring less to make it a smaller adult or physically mutilating an incipient reproductive to reduce its reproductive or dispersive ability (e.g. Zimmerman 1983; Peeters & Higashi 1989). After adulthood, dominants may physically harass subordinates in order to reduce their vigour, prevent them from mating (e.g. Michener 1990) or disrupt their independent breeding attempts (e.g. Emlen & Wrege 1992). All else being equal, manipulative behaviours which are least costly to dominants (i.e. with a low coefficient of manipulation investment) and most effective in causing subordinates to stay and help effectively (i.e. with a low coefficient of helping impairment) should evolve most readily, although higher costs need not preclude social group formation.

Manipulation by a reduction in food levels before adulthood and manipulation by harassment after adulthood appear to be the most common forms of coercion in nature. A reduction in food levels to make an offspring smaller is a simple and inexpensive process for most parents. For example, in aculeate Hymenoptera the size of pollen balls constructed by the mother or the amount of food fed directly to the larvae determines offspring size and sometimes caste (e.g. Plowright & Jay 1968; Packer & Knerer 1985; Gadagkar *et al.* 1988, 1990; Frank & Crespi 1989; O'Donnell 1998; see also Field & Foster 1999). Moreover, among species of halictine bees, there is a close positive association between the extent to which subordinate workers are smaller than their mother, worker subfertility and female bias of the first brood (indicative of less dispersal by first-brood females or less queen supersedure) (Ordway 1965; Plateaux-Quenu 1967; Breed 1975, 1976). These factors are all believed to be under maternal control (Michener & Brothers 1974; Packer & Knerer 1985). Smaller workers are also apparently easier for mothers to control with regard to reproduction (Kukuk & May 1991; Richards & Packer 1994; Richards *et al.* 1995) and probably also have poorer prospects for independent breeding. In other social Hymenoptera, body size is positively correlated with success in independent breeding for overwintering queens (e.g. Owen 1988). Similarly, in naked mole-rats, workers are generally smaller than reproductives and specialized disperser morphs are particularly large (O'Riain *et al.* 1996), which suggests that small size does not overly reduce helper efficiency and dispersal success increases with size. These findings indicate that the assumptions of our model appear to be met in many invertebrates as well

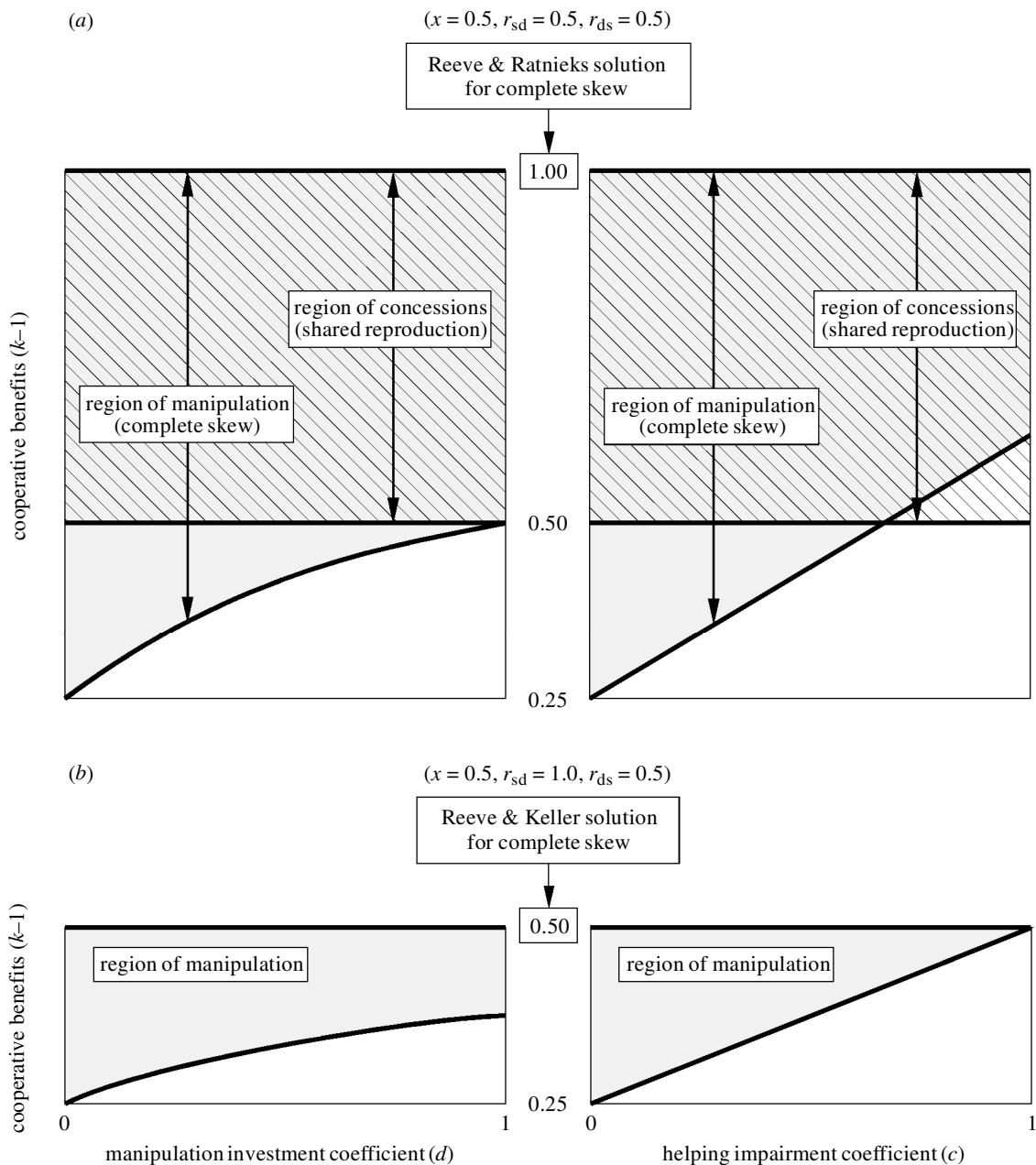


Figure 1. A graphical comparison between manipulation predictions (shaded) and concession predictions (hatched) when the relatedness is (a; sibling) symmetrical or (b; parent-offspring) asymmetrical and when the ecological constraints (x) equal 0.5. The overall qualitative predictions do not differ in relation to the degree of ecological constraints. Reeve & Ratnieks (1993) predicted complete skew only when the cooperative benefits ($k-1$) equal one, with the proportion of reproduction conceded increasing as the cooperative benefits decrease (to the limit of 0.5). Social groups exhibiting complete skew can evolve from manipulation when the cooperative benefits ($k-1$) are as low as 0.25 (when $x = 0.5$), in addition to arising throughout the entire range of concession predictions. Reeve & Keller (1995) predicted the formation of simple matrilineal groups ($r_{sd} = 1.0$) with complete skew when the cooperative benefits ($k-1$) are 0.5 (when $x = 0.5$) but, again, groups evolving via manipulation can form when the cooperative benefits ($k-1$) are as low as 0.25.

as some vertebrates, particularly in cases where pre-emptive manipulation of the offspring food supply is possible at low cost to dominants and the production of helpers versus dispersers is predictably linked to life-cycle phenology, such that manipulated dispersers with low fitness are not produced. Indeed, producing offspring when dispersal opportunities are suboptimal can itself be viewed as a form of manipulation.

Physical harassment of subordinates by dominants appears to be common in both invertebrates and vertebrates (e.g. Michener & Brothers 1974; Emlen 1982; Reyer

et al. 1986; Abbott 1987; Clutton-Brock & Parker 1995; Creel & MacDonald 1995). Such interactions have previously been interpreted as either (i) signals from the dominant to the subordinates that the dominant is vigorous and still fully reproductive (Alexander *et al.* 1991; Crespi 1992; Keller & Nonacs 1993), (ii) aggressive monitoring of subordinate reproduction by the dominant, whereby dominants provide a continual threat to subordinates that any reproductive behaviour will elicit punishment (Brothers & Michener 1974; West-Eberhard 1981), or (iii) activation of 'lazy' subordinates to resume

helping (e.g. Breed & Gamboa 1977; Reeve & Gamboa 1983, 1987; Reeve 1992; Premnath *et al.* 1995). We propose that restrained aggression of dominants toward subordinates often represents a form of manipulation. By this hypothesis, the dominant reduces the ability of subordinates to breed independently should they try to do so by diminishing their energy reserves and reproductive abilities, while causing a relatively minor reduction in their ability to help. Such a differential reduction in helping versus dispersing ability is plausible because helping is normally a less challenging and risky option for subordinates than attempting independent reproduction. Manipulative harassment may also reduce the fighting ability of subordinates relative to dominants and thereby increase the range of conditions for stable cooperation when takeovers by fighting are an available option (see Reeve & Ratnieks 1993).

Manipulation should be particularly common in parent-offspring situations for several reasons (Alexander 1974; Trivers 1974). First, parental care, which represents a universal antecedent to alloparental care and eusociality (Alexander *et al.* 1991), has evolved in the context of maximizing parental rather than offspring inclusive fitness. As such, the imposition of costs on some offspring is just another means to this end. Second, parents virtually always have considerable control over the physical and psychological development of their offspring and, thus have the power to sculpt offspring life histories for their own benefit. Such parental manipulation could even involve exploiting offspring parental tendencies, such that parental care is expressed in situations which are not adaptive for their offspring (Jamieson 1989, 1991). Third, parents are older and more experienced than their offspring (e.g. Emlen 1996; Clutton-Brock 1998) and may thus often be able to dominate them even after they reach maturity. Finally, offspring should often readily submit to manipulation by their parents, because in simple parent-offspring societies the offspring may gain equally from sib-rearing and offspring rearing, but parents may gain a twofold advantage from sib-rearing (Charnov 1978; Stubblefield & Charnov 1986). Parents should therefore be willing to impose substantial costs on their offspring to increase the frequency of sib-rearing and offspring who reduce the negative inclusive fitness effects of manipulation by submitting at minimal cost to their parents and themselves should be favoured.

In semi-social, multiple-foundress situations, manipulative-control asymmetries should be less than for parents and offspring, opportunities for independent breeding should be higher because the associations form at the usual time in the life cycle for reproduction and relatednesses are symmetrical. As a result, stable associations due to manipulation are expected to be less common in these circumstances, because higher costs must be imposed on subordinates to coerce helping and higher cooperative benefits are needed to make helping a favoured option.

The most important divergent prediction between our model and concession models is that the skew can be complete under our model when cooperative benefits, relatedness or both are low relative to the concession model requirements. In most primitively eusocial and cooperatively breeding Hymenoptera, it appears that helpers indeed help (e.g. Strassmann & Queller 1989;

Hogendoorn & Velthuis 1993; Bull & Schwarz 1996), but that colony productivity increases at a decreasing rate as helper number increases (Michener 1964; Kukuk & Sage 1994). In most of these species where reproduction has been quantified or inferred, the skew appears to be high when the mother queen is present (Packer & Owen 1994; see the review in Reeve & Keller (1995)) and some such species exhibit relatedness levels which are sufficiently low to draw concession model predictions into question (Strassmann *et al.* 1989, 1994; Ross & Carpenter 1991; Hughes *et al.* 1993; Field *et al.* 1998). However, in no cases have all of the variables relevant to testing the model been measured. Unique, testable predictions of our model include (i) differential 'manipulative' treatment towards potential group members which results in deprived or harassed individuals staying and helping, (ii) a reduction in the dispersal or breeding capabilities of manipulated subordinates, and (iii) the presence of societies, particularly matrilineal ones, with high or complete skew and low productivity benefits or relatedness relative to the concession predictions, although the manipulation model also allows high productivity and relatedness. In some taxa, it may also be possible to manipulate potential subordinates experimentally and test for the expected changes in helping versus dispersing.

One limitation of the manipulation model is that it assumes that subordinates cannot avoid dominant-imposed costs, when subordinates should often be under selection to escape manipulation by dominants. If manipulative acts pre-empt escape (e.g. feeding juveniles less), then such selection cannot be effective. In contrast, if manipulation involves ongoing behavioural interactions, such as frequent aggressive nudging or enforced displays of subordinate status, then subordinates might be expected to have the option of avoiding the interactions as best they can and perhaps thereby improving their dispersal prospects. In many social insect species, subordinates attempt to avoid the dominant while at the nest site (Buckle 1982; Michener 1990). This behaviour could be interpreted as avoidance of reproductive suppression, aggressive manipulation or both. Moreover, in some halictine bees, some first-brood offspring of the foundress avoid her by entering diapause directly and becoming next year's foundresses rather than this year's workers (Yanega 1988). Has such early diapause evolved in part as a means of escaping maternal manipulation? In *Halictus rubicundus*, directly diapausing, first-brood offspring are larger than sibs which stay at home to help (Yanega 1989), which is consistent with the idea that small worker size tilts behavioural choices towards helping. In other halictines, most first-brood offspring stay and help, while some leave and attempt to breed independently in the same year (Stockhammer 1967; Sakagami & Hayashida 1968; Sakagami 1977); the presence of such species shows that the strategies envisioned by our model are realistic and can be investigated in natural populations.

Another limitation of our model is that manipulation by itself cannot drive the origin of helping, because the initial stage of producing less-vigorous offspring could not be favoured by selection in the absence of some degree of helping which evolved by some other means (Charlesworth 1978; Craig 1979, 1983). This consideration limits the applicability of manipulation models to facilitation of the

origin of helping or maintenance of helping which would otherwise be lost (e.g. Wcislo & Danforth 1997). However, we note that even a low frequency of helping should be rapidly capitalized upon by manipulative mothers, because their fitness returns are so high from replacing grandoffspring with offspring or nephews and nieces with sibs (Charnov 1978; Stubblefield & Charnov 1986).

Our model cannot explain situations with low skew, because we have assumed that the manipulative ability of dominants is complete. Concession models predict that low skew arises where r or α are low, such that dominants must offer higher concessions to subordinates to retain their services. This prediction leads to the intraspecific and interspecific association between r and skew which has been interpreted as evidence for these models (Keller & Reeve 1994). We believe instead that low skew and low relatedness often coincide in cases where dominance itself is an economically unfavourable or inviable strategy, as a result, for example, of similarity in fighting abilities or difficulty in enforcement (e.g. Vehrencamp 1978, 1983a,b; DeLay *et al.* 1996; Getz & McGuire 1997; McConnell-Garner & Kukuk 1997). In such situations, dominance-subordinate relations *per se* do not exist, neither concession nor manipulation models apply and models with different assumptions are required. Moreover, a lack of complete skew in nature cannot be considered as evidence against the applicability of our manipulation model, because it may be due to incomplete manipulation, taxon-specific factors (Clutton-Brock 1998) which are not considered here or, perhaps, some combination of manipulation and concession.

What are the implications of our model for the development of a general social evolution theory based on skew models? Where the interests of social organisms coincide, mutualistic benefits favour cooperation but, when interests conflict, one individual can seek to bend another to its will by either force (taking control of behaviour away), persuasion (providing benefits to cooperators) or coercion (imposing costs on non-cooperators) (Brown *et al.* 1997). Concession models rely on persuasion, while punishment models (e.g. Clutton-Brock & Parker 1995), policing models (e.g. Reeve & Keller 1997) and our manipulation model are based on coercion. We have shown that under most ecological and genetic conditions, it is better for dominants to impose costs and instil fear than to concede the love of shared reproduction. Whether fear, love or both prevail in nature remains to be determined.

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