A commitment model of reproductive inhibition in cooperatively breeding groups

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Cooperatively breeding groups include individuals that give up some current reproductive opportunities while remaining in a group. In some cases, these individuals are physiologically or morphologically unable to reproduce. Empirical and theoretical evidence suggest that this inability often does not result from stress or manipulation by dominants against the interests of subordinates. I argue that such reproductive inhibition can represent a commitment not to reproduce in exchange for a reduction in costs imposed by dominants. I present a model that allows subordinates to choose whether to inhibit their own reproduction ("self-inhibition") and accept no direct reproduction while in the group or to remain flexible and attempt to take a share of group productivity. If dominants assess the reproductive status of subordinates and punish those that reproduce, this model predicts self-inhibition when group members are closely related, opportunities for independent breeding are poor, assessment of reproductive status and eviction are costly, and the chance of being detected when cheating is high. However, dominants are less likely to assess the reproductive status of subordinates that are closely related, resulting in a narrow window of relatedness in which self-inhibition is favored. Counterintuitively, this window is wider when flexible subordinates would be able to take a large share of group production. Although the model assumes that dominants are able to reliably detect commitment, it is generally robust against mistakes in the form of dominants failing to assess uncommitted subordinates, or even low frequencies of deception by flexible subordinates. *Key words:* credibility, imperfect information, reproductive skew, reproductive suppression. *[Behav Ecol 15:585–591 (2004)]*

Cooperative breeding and eusociality are taxonomically widespread, occurring in social arthropods (including ants, wasps, bees, thrips, aphids, termites, beetles, shrimp, and spiders; see Choe and Crespi, 1997; Duffy, 1996), colonial invertebrates (Rinkevich and Shapira, 1999), mammals (Solomon and French, 1997), birds (Stacey and Koenig, 1990), fish (Taborsky, 1985), and bacteria (Crespi, 2001). All of these societies include some individuals that forgo some or all of their current reproductive opportunities to join or remain in a group alongside reproductively active individuals. By doing so, they may avoid costs of dispersal, increase the production of offspring by relatives, gain experience in raising young, gain priority of access to future territories or mates, or parasitize breeding opportunities (Alexander et al., 1991; Emlen, 1995; Emlen and Vehrencamp, 1985; Vehrencamp, 1983).

In these groups, subordinate reproduction is inhibited, either permanently, in the case of advanced eusocial organisms, or in the presence of dominants. The mechanism leading to reproductive inhibition varies among and within species. Often, inhibition is strictly behavioral; that is, subordinates are capable of reproducing while in the group, but they do not reproduce or do so less than dominants (e.g., male dwarf mongooses; Creel and Waser, 1997). In other systems, inhibition has a morphological or physiological basis, so that inhibited subordinates are unable to reproduce (see Choe and Crespi [1997] and Solomon and French [1997] for examples among social arthropods and mammals). Such inhibition may result from direct manipulation by dominants. Dominant social insects may feed subordinates that will become workers less than they do those that will become

reproductives, suppressing workers' reproductive development (reviewed in Crespi and Ragsdale, 2000). However, physiological inhibition often depends on the receipt of chemical or other cues from the dominant and is mediated through the subordinate's endocrine system. As argued by Keller and Nonacs (1993), it is unlikely that such inhibition involves direct chemical manipulation against the interests of the subordinate. Otherwise, subordinates that did not respond to manipulative or misleading cues from dominants would receive higher fitness payoffs than those that did, and failure to respond to the cue could invade the population. There is also little evidence that such inhibition is a consequence of stress associated with subordinate status (e.g., French, 1997; Mays et al., 1991). Thus, many instances of physiological or morphological inhibition likely reflect self-restraint rather than dominant suppression of reproduction. I hereafter refer to these as instances of "self-inhibition."

Physiological or morphological inhibition, whether imposed by dominants or resulting from self-restraint, is not a requirement for cooperatively breeding societies. In many social Hymenoptera, subordinate workers remain capable of producing male offspring but often do not, likely because of worker policing (e.g., Foster and Ratnieks, 2001). As discussed earlier, behavioral mechanisms alone can produce the unequal division of group reproduction characteristic of these societies. There would seem to be a benefit to remaining reproductively flexible because it would allow subordinates to cheat, if they can do so and remain undetected. Given this benefit, why do subordinates in some societies relinquish the option of reproducing, at least while they remain in the group?

One potential benefit of physiological or morphological self-inhibition of reproduction may be reduced costs of harassment or eviction from the group. In game theory terminology, self-inhibition would then represent a *commitment* (Schelling, 1960), in which one player (i.e., the subordinate) gives up some of its behavioral options (i.e., reproducing

while in the group), and thereby influences the behavior of other players (i.e., harassment and eviction by the dominant). Importantly, such a commitment must be credible to be effective (Schelling, 1960). In terms of reproductive self-inhibition, credible commitment means that a self-inhibited subordinate must remain so if the dominant cooperates (that is, does not attempt to harass or evict the subordinate), and it must communicate this commitment honestly to other players. Because there should be an incentive for the subordinate to cheat (by reproducing at a cost to the dominant) if the dominant cooperates, the first condition requires that self-inhibition be difficult to reverse, at least in the short term. Importantly, self-inhibition does not necessarily require that subordinates never reproduce, only that they do not reproduce while they are accepted by dominants. The second condition requires that other group members can reliably detect self-inhibition. Both of these likely apply in at least some instances of physiological and morphological inhibition. Development of reproductive capacity upon leaving the group can be costly in terms of time (e.g., Clarke et al., 2001) or impossible, and dominant breeders often can chemically or visually detect physiological or morphological inhibition (e.g., van der Westhuizen et al., 2002). Commitment is a prevalent feature of strategic games among humans (Nesse, 2001; Schelling, 1960) but has generally not been invoked in game-theoretic explorations of animal behavior (but see Adams, 2001; Dugatkin, 2001; Silk, 2001), in part because of the requirement of honest communication of commitment to other players (Maynard Smith, 1982).

In this paper, I present a model that addresses the evolutionary stability of reproductive self-inhibition as a commitment. I address when reproductive inhibition can be stable against invasion by the tactic of remaining reproductively flexible. Inhibition could be favorable to subordinates if it resulted in reduced costly assessment by dominants, particularly if group-produced offspring of subordinates are of low quality because of inbreeding depression, maternal effects, or competition with dominant offspring. I also use the model to address how credible the cues of inhibition must be for a commitment to be effective. Hirshleifer (2001) has shown that perfect credibility is not necessary for a commitment to be believed in economic games. I demonstrate that a commitment to reproductive self-inhibition can be evolutionarily stable even if dominants that would normally assess uncommitted subordinates sometimes inadvertently fail to do so. This model is based on concession-based optimal skew models (Keller and Reeve, 1994), which predict reproductive division in groups with respect to social and ecological variables, but it differs from previous models in its assumption of how inequality within groups is maintained (dominant control versus subordinate self-inhibition). In addition to demonstrating how a commitment framework can explain the distribution of reproductive inhibition in cooperatively breeding groups, the self-inhibition model suggests that the widely used concession-based optimal skew framework is only applicable under a limited range of conditions, which may explain the equivocal support for those models (Field et al., 1998; Keller and Reeve, 1994).

MODEL

The model is based on concession-based optimal skew models (Keller and Reeve, 1994; Vehrencamp, 1983). Optimal skew models integrate the effects of opportunities for dispersal, group productivity, future rewards, and inclusive fitness to predict the monopolization of reproduction by dominant individuals (reproductive skew) in group-breeding organisms (Keller and Reeve, 1994; Ragsdale, 1999; Vehrencamp, 1983).

In concession-based models, the reproductive skew, or monopolization of reproduction by dominants, results from the decisions of both dominant and subordinate group members, and it reflects a 'social contract,' in which dominants and subordinates agree on the direct reproduction allocated to subordinates. For a subordinate, the decision to stay in the group or to disperse will depend on the indirect benefits of helping kin and any direct reproduction that it receives while in the group. Therefore, dominants may be willing to concede some direct reproduction to subordinates if grouping improves the production of offspring by dominants and offering a concession increases the probability that the subordinate stays. If the direct reproduction offered by dominants equals or exceeds that required by subordinates, groups form. The actual reproductive concession is then the minimum proportion of direct reproduction, if any, required to keep the subordinate from leaving the group. These models predict that high skew societies, such as those of cooperative or eusocial breeders, are expected when group members are related, opportunities for independent breeding are poor, the benefits of grouping are high (reviewed in Keller and Reeve, 1994), and when future rewards are great (Ragsdale, 1999).

Concession-based skew models generally assume that the dominant has complete control over subordinate reproduction. This implies that subordinates are unable to violate the social contract. However, there is no clear empirical evidence for complete dominant control (reviewed in Clutton-Brock, 1998). The potential for violation of the social contract is problematic to skew models. At the concession specified by the social contract, subordinates should be tempted to cheat, if they can, by increasing their direct reproduction at a cost to the dominant. This may lead to a 'tug-of-war' between dominants and subordinates over the division of reproduction (Reeve et al., 1998).

In this model, reproductive self-restraint, rather than dominant suppression, is the mechanism that prevents violation of the social contract by subordinates. In Figure 1, I present the model as a game in extensive form. Dominants must decide whether to accept or evict subordinates and whether to assess subordinates. Assessment is defined as the investment of time and energy, at a cost to the dominant, in attempting to determine whether flexible subordinates are reproducing, and punishing them if they are. Thus, in this model, the term 'assessment' includes both the acquisition of information on subordinate reproduction and the action of punishing reproducing subordinates. Subordinates must decide whether to stay with the dominant or to breed alone, and whether to commit to reproductive self-inhibition or to remain reproductively flexible. If they are flexible, they must decide whether to cooperate with the dominant and accept the reproduction, if any, conceded, or to cheat by taking a greater share of reproduction at a cost to the dominant. Below, I present model parameters, which are summarized in Table 1, and describe the stable solutions to the game. The payoffs for each combination of tactics are summarized in Table 2.

I base the model on the simplest skew model, which presents a game between one subordinate and one dominant (Keller and Reeve, 1994; Vehrencamp, 1983). Because physiological and morphological inhibition often involves a complete cessation of direct reproduction while in the group, I assume that dominants do not allocate any reproduction to subordinates. The important parameters in the basic skew model are then the expected success of a subordinate attempting independent breeding (x), the ratio of group production to that of a solitary dominant ($k > 1$), and the relatedness between dominant and subordinate (r).
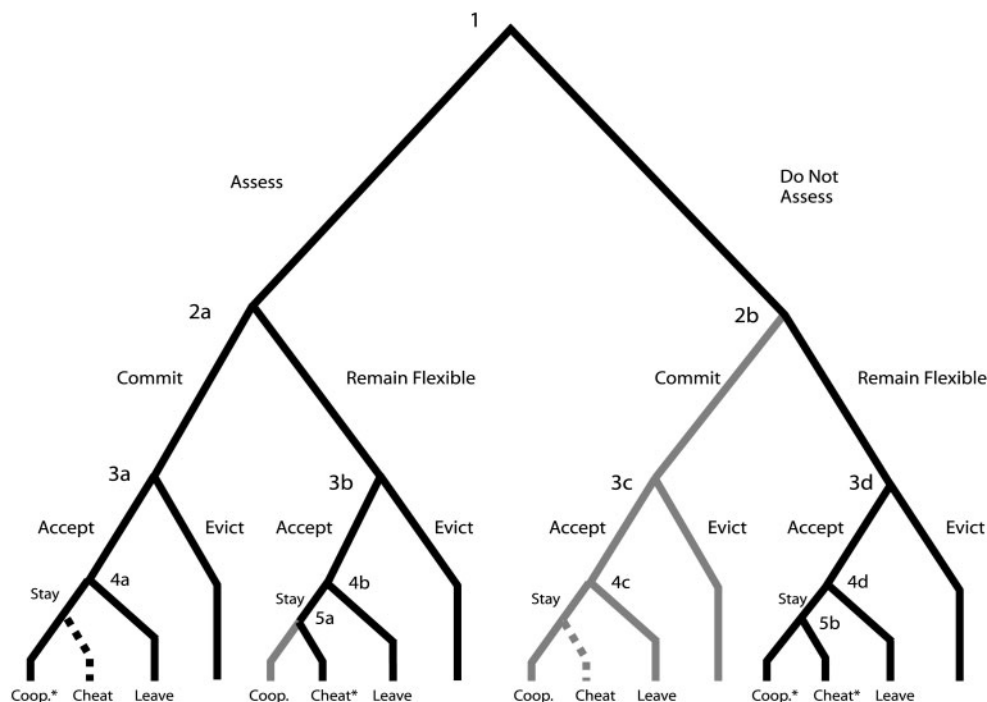
Figure 1
Full reproductive self-inhibition game in extensive form. Dashed lines indicate tactics that are not available to committed (self-inhibited) individuals. Grey lines indicate branches of the game that cannot include evolutionarily stable equilibria. Assuming that subordinates will stay in the group (and be allowed to by dominants), there are only four possible evolutionarily stable equilibria, which are marked with asterisks.

The model presented here differs from previous skew models because subordinates may commit to reproductive self-inhibition. If they do, the payoffs to a dominant and a subordinate when breeding as a pair or alone (see Table 2) are similar to those described in the basic skew game, with two modifications. First, I assume that the expected success of a subordinate that is evicted or leaves the group is lower when it is committed to reproductive self-inhibition (x_c) than when not (x_u). Development of reproductive capability is unlikely to be instantaneous. Clarke et al. (2001) found that reproductively inhibited Damaraland mole-rats (*Cryptomys damarensis*) began to mate about 30 days after being separated from the group and paired with an unrelated male, whereas reproductively capable females (i.e., queens) began to mate about 10 days after separation from the group. In some cooperatively

breeding systems, subordinates face an increased risk of mortality when they leave the group, (e.g., Balshine-Earn et al., 1998). When both of these are true, the probability of dying between leaving the group and beginning to reproduce independently will be higher for committed subordinates than for uncommitted ones.

Second, I also allow group-produced offspring of the subordinate to be of poorer quality than those of the dominant. This may be a result of inbreeding depression, if the only available mates for a subordinate that remains in the group are close relatives (French, 1997). Other possible mechanisms for this difference include heritable or maternal effects of quality (i.e., genotypically or phenotypically poor quality individuals produce poor quality offspring), or competition between offspring of subordinates and older

Table 1
List of parameters in the model

Symbol	Description of parameter
r	Relatedness between dominant and subordinate
x	Direct fitness of a subordinate that leaves or is evicted from the group
x_c	Direct fitness of a committed (self-inhibited) subordinate upon leaving the group
x_u	Direct fitness of an uncommitted (flexible) subordinate upon leaving the group
k	Ratio of the total offspring production by a group consisting of one dominant and one subordinate to that of a lone dominant
v	Ratio of the value of group-produced offspring of subordinates to those of a dominant
q	Proportion of total group reproduction that consist of direct reproduction by a cheating subordinate
f	Probability that an assessing dominant detects a cheating subordinate
m	Ratio of the total offspring production by a group with an assessing dominant to that of a group with a dominant that does not assess
δ	Probability that a dominant erroneously fails to assess when subordinates are uncommitted (flexible)
r_a	Threshold value of relatedness, below which dominants assess
r_i	Threshold value of relatedness, above which subordinates are self-inhibited, when dominants always correctly identify flexible subordinates
r_d	Threshold value of relatedness, above which subordinates are self-inhibited, when dominants make errors in identifying flexible subordinates.

Table 2
Fitness payoffs for each combination of dominant and subordinate tactics

Dominant	Subordinate	Dominant	Subordinate	Dominant Payoff	Subordinate Payoff
Assess	Commit	Evict		$1 + rx_c$	$x_c + r$
		Accept	Cooperate	k	rk
			Leave	$1 + rx_c$	$x_c + r$
	Flexible	Evict		$1 + rx_u$	$x_u + r$
		Accept	Cooperate	mk	rmk
			Cheat	$(1 - f)mk(1 - q) + f$ $+ r[(1 - f)vmkq + fx_u]$	$(1 - f)vmkq + fx_u$ $+ r[(1 - f)mk(1 - q) + f]$
			Leave	$1 + rx_u$	$x_u + r$
Does not assess	Commit	Evict		$1 + rx_c$	$x_c + r$
		Accept	Cooperate	k	rk
			Leave	$1 + rx_c$	$x_c + r$
	Flexible	Evict		$1 + rx_u$	$x_u + r$
		Accept	Cooperate	k	rk
			Cheat	$k(1 - q) + rvkq$	$vkq + r(1 - q)$
			Leave	$1 + rx_u$	$x_u + r$

ones of dominants (Ridley and Sutherland, 2002). The value of group-produced offspring of subordinates relative to those of dominants is described by v ($v \leq 1$).

If the subordinate does not commit to reproductive self-inhibition, then it can attempt to cheat. If it does so, it attempts to steal a proportion, q, of the group's direct reproduction for itself, by producing its own offspring at a cost to those of the dominant. If the dominant has decided to assess whether subordinates are reproducing, this attempt will be detected with some probability, f, and the subordinate will be evicted if cheating is detected. I assume that assessment by the dominant is costly in terms of time, energy, and stress, leading to decreased group productivity. The ratio of productivity between pairs with flexible and inhibited subordinates is m. Although I do not present them here, the results are qualitatively the same if direct costs to subordinates replace the cost to group productivity (unpublished model results). The payoffs for dominants and subordinates in the absence of commitment to reproductive self-inhibition are presented in Table 2.

If subordinates never cheat, why should dominants assess subordinate reproduction at all, if doing so is costly? For assessment to be evolutionarily stable, it must be costly to dominants only when subordinates are likely to cheat (i.e., are not committed). This requires that dominants have reliable information on the reproductive ability of subordinates and respond to these cues appropriately by paying the costs of assessment when subordinates are flexible, but not assessing when subordinates are self-inhibited. However, as discussed later, this information does not need to be perfect.

Returning to Figure 1, the game can be simplified substantially, because there are several possible combinations of tactics that can never be evolutionarily stable. For example, if dominants assess, subordinates will never remain flexible and still cooperate (node 5a in Figure 1). This is because remaining flexible is costly for subordinates (through the costs of assessment for related dominants). Therefore, if a subordinate were to cooperate, it would always do better by committing when dominants assess flexible subordinates.

If dominants do not assess, self-inhibition by subordinates can never be evolutionarily stable when the expected success of committed subordinates that leave or are evicted from the group, x_c, is less than that of uncommitted ones, x_u. When this is so, all possible payoffs to subordinates are equal or lower if they commit than if they do not. In other words, commitment to self-restraint in the absence of assessment cannot be an

evolutionary stable strategy (ESS) if self-inhibition is costly upon leaving the group (node 2b on Figure 1).

To simplify the problem further, I assume that subordinates are willing to stay in the group and that dominants will let them do so if they do not cheat. Inspection of the payoff functions in Table 2 reveals that this will be so when dispersal costs are high (x_c and x_u are low) or when group productivity (k) is high. Given that, there are only four possible ESS solutions to the game (Figure 1). If dominants assess, subordinates may either commit and cooperate or remain flexible and cheat. If dominants do not assess, subordinates will always remain flexible but may either cooperate or cheat.

If subordinates cheat, dominants should attempt to assess whether subordinates are cheating when relatedness between the dominant and the subordinate, r, is less than a threshold value, r_a. That is, $r < r_a$, where

$$r_a = \frac{f - k(1 - q)[1 - m(1 - f)]}{vkq[1 - m(1 - f)] - fx_u}$$

If subordinates cooperate, the payoffs to assessing and not assessing are equal. However, if $r < r_a$, the only evolutionarily stable tactic is to assess, whereas if $r > r_a$, assessing cannot be evolutionarily stable. Therefore, regardless of the decision of subordinates, the threshold for assessment is always the same.

If dominants do not assess subordinate reproduction, subordinates should cooperate (but remain flexible) if the relatedness between dominant and subordinate, r, is greater than the value of group-produced offspring of the subordinate, v. If relatedness is greater than this value, subordinates gain more through the indirect benefits of raising the offspring of dominants than they would through any direct reproduction in the group. If dominants do assess (i.e., when $r < r_a$), then subordinates should be self-inhibited (and therefore cooperate) if relatedness exceeds a threshold, r_i, where

$$r_i = \frac{fx_u + vmkq(1 - f)}{k - f - mk(1 - f)(1 - q)}$$

This threshold value decreases when cheating yields poor returns if successful (the value, v, and amount, q, of direct reproduction by the subordinate are low) and is easily detected (f is high; Figure 2). This value also decreases when the relative value of group to solitary breeding is high (high

group production of offspring, k, poor success of dispersing flexible subordinates, x_u) and assessment is costly (m is low). Note that the success of a self-inhibited subordinate that leaves the group (x_c) does not influence this threshold.

From the threshold values r_a and r_i, it can be seen that many of the same conditions that favor inhibition (e.g., high relatedness) do not favor assessment. As a result, the window of relatedness in which inhibition is expected ($r_a - r_i$) may be narrow (Figure 2). The width of this window decreases with increasing value of group productivity (k) and costliness of assessment (decreasing m), and it increases with decreasing quality of group-produced offspring of subordinates (v) and increasing probability of detecting cheaters (f; Figure 2). Interestingly, the width of this window increases with increasing q, the direct reproduction by a cheating subordinate. Although subordinates that remain flexible (and cheat) receive a high payoff when q is high, the amount of cheating by subordinates has a strong effect on whether dominants assess, resulting in a wider window of self-inhibition (Figure 2B).

IMPERFECT INFORMATION

The model is robust to a degree of violation of the assumption that dominants have perfect information regarding subordinate commitment and that they then behave appropriately. Whether commitment can be maintained despite imperfect information or incorrect responses depends upon the direction of mistakes made by dominants.

Suppose that dominants occasionally do not attempt to assess reproduction by a subordinate, even though it is uncommitted and could potentially cheat, with some probability, δ. If this is the case, the threshold relatedness, r_a, below which dominants should assess, does not change. Thus, the conditions that favor assessment by dominants are not influenced by the probability of erroneously failing to assess a flexible subordinate. The decisions of subordinates are influenced by this failure. A subordinate should commit when relatedness to the dominant, r, exceeds a threshold value, r_d, where

$$r_d = \frac{(1 - \delta)A + \delta vkq}{(1 - \delta)B + \delta kq}$$

and A is the numerator and B the denominator from r_i, the threshold for commitment when there are no mistakes. As shown in Figure 2C, the window in which commitment can evolve is smaller when mistakes are made, but it is still present.

Commitment is not robust to mistakes in the opposite direction. If dominants sometimes still engage in costly assessment even though subordinates are committed, then dominants that do not assess will receive a higher payoff than those that do. Therefore, dominants should not assess. As discussed earlier, if dominants do not assess, then commitment cannot be stable when the cost of dispersal is greater for committed subordinates than those that remain flexible, that is, when $x_c < x_u$.

DISCUSSION

This model demonstrates that reproductive self-inhibition by subordinates can evolve in exchange for reduced risks of harassment and eviction by dominants. This explanation for reproductive inhibition does not require that dominants manipulate or mislead subordinates into acting against their own interests, nor does it require complete dominant control of subordinate reproduction (or even perfect information regarding subordinate self-inhibition). This framework pre-
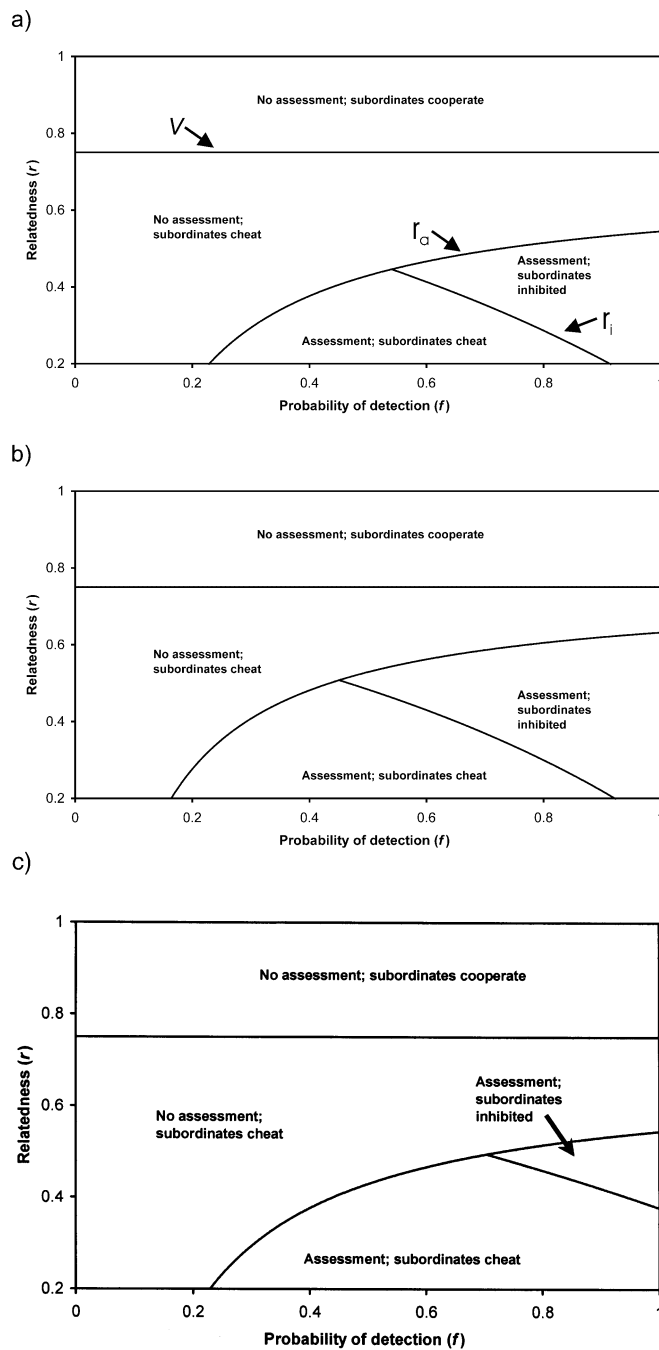

Figure 2
The influences of relatedness (r), probability of being detected if cheating (f), potential theft by cheating subordinates (q), and imperfect honesty of signals (δ) on assessment and self-inhibition. (a) Dominants can always correctly identify committed and flexible individuals ($\delta = 0$, $q = 0.45$, $v = 0.75$, $k = 1.4$, $m = 0.95$, $x_u = 0.05$). (b) As in (a), but the maximum amount that subordinates can steal is higher ($q = 0.5$). (c) As in (a), but dominants mistakenly fail to assess flexible subordinates with probability, $\delta = 0.3$).

dicts that unequal division of reproduction resulting from self-inhibition of subordinates is more likely to occur when group members are related, cheating is easily detected, and when the quality of subordinate offspring is poor, assuming that dominants assess subordinate reproduction and punish subordinates that reproduce. However, many of the condi-

tions that favor self-inhibition (high relatedness, high cost of assessment) do not favor assessment. Therefore, the window in which self-inhibition is expected may be small.

This model corresponds with concession-based skew models when subordinates inhibit their own reproduction. In dwarf mongooses, skew models have been successful in predicting the division of reproduction among females, in which subordinates may be physiologically inhibited (Creel and Waser, 1997). These models have been less successful for males, which are not physiologically inhibited (Creel and Waser, 1997). The present model suggests that the predictions of concession-based skew models will only apply under a narrow range of parameters (Figure 2) and will often not be applicable under some of the very conditions that are expected to promote group living under high skew (e.g., high relatedness, r; high group benefits, k).

The model assumes that assessment of subordinates is costly, reproductive inhibition reduces these costs, and reliable cues of self-inhibition exist. Corticosterone stress hormones are higher for dominants than subordinates in many cooperatively breeding animals but not in other dominance-structured groups (Creel, 2001), suggesting that the dominant position can be costly in cooperatively breeding societies. Assessment of subordinates may be one reason for this stress. In naked mole-rats, harassment in the form of 'shoving' by queens is positively correlated with plasma luteinizing hormone concentrations of recipients, and thus with their ability to reproduce (van der Westhuizen et al., 2002). If this shoving were costly to queens and/or recipients, these costs would be reduced when subordinates are inhibited.

It is not clear in this example whether mole-rat queens can detect reproductive hormone concentrations themselves or use other cues that are correlated with reproductive inhibition. However, the concentration of reproductive hormones is likely to be a reliable cue of flexibility versus physiological inhibition, as it would be difficult to fake or mask. Self-inhibition may be more likely in societies where such information is available than in those where dominants must rely on visual cues.

A further assumption of the model is that subordinates that commit do not reproduce at all. However, it may be possible to commit to reduced reproduction rather than to no reproduction. Incorporating this possibility into the model does not change its qualitative predictions (unpublished modeling results). Assuming that subordinates do not reproduce at all while in the group also addresses a potential problem with reproductive skew models. Recently, it has been argued that reproductive skew models may not be evolutionarily stable when subordinates have imperfect knowledge of the share of reproduction that will be conceded by dominants (Kokko, 2003). If subordinates have imperfect knowledge, they should decide whether to stay based on the share of reproduction offered by the average dominant in the population rather than that offered by any particular dominant. When this is the case, any given dominant gains by reducing the amount of direct reproduction that it concedes. Eventually, this may result in the abandonment of group breeding, as concessions decline towards zero (Kokko, 2003). In the current model, only those conditions under which subordinates will remain in the group without any concessions are of interest. Dominants cannot reduce concessions further, and they gain no benefit from increasing concessions. Therefore, the formation of groups without concessions can be an ESS.

The model makes several general predictions regarding expected patterns of cooperation and reproductive inhibition in cooperative breeding organisms. These are discussed below.

(1) Reproductive self-inhibition is more likely when subordinates are closely related to dominants (as long as dominants assess) and when cheating by subordinates is easily detected. In mammals, females tend to be physiologically inhibited, while males are not (Mumme, 1997). The self-inhibition model may explain this pattern in two ways. First, the relatedness of males to the dominant male may be generally lower than that of females to the dominant female, because of uncertain paternity or male dispersal (Creel and Waser, 1997). Second, cheating by females may be more easily detected than that by males because of the lengthy gestation period.

(2) Reproductive self-inhibition is more likely when the offspring of subordinates are of relatively poor quality. Physiological inhibition in several mammals and birds (Mays et al., 1991; Carter and Roberts, 1997; French, 1997; Reyer et al., 1986) is correlated with the relatedness of potential mates in the group. This pattern has been attributed to inbreeding avoidance, which does not conflict with the predictions of this model. However, in this model, inbreeding depression (or any other mechanism leading to poor quality group-produced offspring of subordinates) is not, by itself, sufficient to explain inhibition when the costs of dispersal are greater for committed subordinates than for flexible ones (i.e., when $x_c < x_u$). The threat of punishment by the dominant must also be present, because self-inhibition, as opposed to simply not breeding but remaining flexible, can only be an ESS when dominants assess.

This effect of the quality of subordinate offspring reconciles reproductive self-restraint with the possibility of dominant manipulation (see also Crespi and Ragsdale, 2000). If dominants can force subordinates to be of poor quality (e.g., by restricting food) and this in turn means that they produce poor quality offspring, self-inhibition may be facilitated.

(3) Self-inhibition among close relatives is more likely when the potential loss of reproduction to subordinates that do not commit is high. Subordinates that can take a large share of group productivity as direct reproduction (q) are less likely to inhibit themselves, all else being equal. However, this effect is slight, while increasing a cheating subordinate's share of direct reproduction has a strong effect on the likelihood of assessment by dominants, with assessment favored at higher values of relatedness between the pair (Figure 2B). Thus, the overall width of the window of commitment is greater when the proportion of direct reproduction that can be stolen by a cheating subordinate is large (Figure 2B).

(4) Perfect information is not necessary for self-inhibition to be evolutionarily stable. This implies that the system can be robust against occasional mistakes by dominants, so long as they are consistently in the direction of mistakenly allowing uncommitted subordinates to escape assessment. Perhaps more interestingly, this also implies that the system is robust to some degree of deception by subordinates, so long as such deception is infrequent and is maintained at low frequency by some other mechanism (such as policing by other subordinates).

I have used a single parameter, x, to describe opportunities for dispersal. This was to focus on the stability of commitment rather than on when groups should form. However, realized opportunities for dispersal represent an interaction between life-history characteristics and the decision to disperse. As such, the relationship between parameters such as survival of dispersing individuals or probability of gaining a territory and the decision to disperse may be nonexistent (Pen and Weissing, 2000) or dependent on delayed-fitness benefits and the mechanism of density-dependence (Kokko and Ekman, 2002; Kokko and Lundberg, 2001; Pen and Weissing,

2000). At the population level, cooperative breeding (and commitment) may be most likely when mutualistic benefits (such as helping of kin) and delayed-fitness benefits are sufficiently high to maintain grouping even when it leads to an increase in vacant positions for breeding (Kokko and Ekman, 2002). Within populations, variation in quality of opportunities for dispersal should still influence the decisions of subordinates (e.g., subordinates should be more likely to stay when they are on high-quality territories, with little option but to disperse to poorer-quality ones, and less likely to stay when on low-quality territories; Kokko and Ekman, 2002; Kokko and Lundberg, 2001). Incorporating density-dependence could strengthen one of the key assumptions about the costs of dispersal in the model, which is that committed subordinates have lower success after dispersal relative to uncommitted ones. If there is intense competition for breeding vacancies, uncommitted subordinates may be able to jump to the head of the queue, because they can begin breeding earlier or may otherwise be better competitors for vacancies. Incorporating these effects into the present model may add the same richness to understanding the decision to commit to a non-breeding position that they have to the basic skew framework.

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