

# TESTS OF REPRODUCTIVE-SKEW MODELS IN SOCIAL INSECTS

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■ **Abstract** Reproductive-skew theory can be broadly divided into transactional models, in which reproduction is shared among group members in return for some fitness benefit, and tug-of-war models, in which reproductive sharing arises solely from an inability of each group member to fully control the others. For small-colony social insects in which complete reproductive control by a single individual is plausible, transactional-concession models account, better than any other existing model, for observed relationships between each of the dependent variables of skew, changes in reproductive partitioning over time, group size, and within-group aggression, and each of the predictor variables of genetic relatedness, ecological constraints on solitary breeding, and benefits of group living. An extension of transactional-concession models via the “workers-as-a-collective-dominant” model potentially offers new insights into some of the most striking reproductive patterns in large-colony eusocial Hymenopteran species, from the loss of worker capacity to produce female offspring to patterns of skew and aggression in polygynous societies.

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## INTRODUCTION

In the last 10 years, much theoretical and empirical attention has focused on factors that influence the evolution of reproductive partitioning among members of animal social groups, in particular on the degree to which reproduction is biased in favor of dominant breeders (5a, 7, 8, 10, 13, 14, 18, 19, 21, 32, 37, 40–42, 47, 51, 54, 71–75, 77–79, 82, 83, 88, 101, 105–107; HK Reeve & RL Jeanne, submitted for publication). In both vertebrate and insect societies, there is tremendous variation in reproductive skew, that is, the degree of reproductive bias in favor of dominant breeders. In high-skew societies, direct reproduction is concentrated in one or a few dominant breeders in the group; in low-skew societies, reproduction is distributed more evenly among group members.

The rapidly growing interest in reproductive-skew theories appears to have two sources. First, evolutionary biologists have realized that a theory that properly integrates our understanding of the ecological, genetic, and social factors that influence skew has the potential to apply widely to many animal societies and even assume the status of a unified theory of social evolution (47, 82). Second, it has been recognized that a theory of reproductive skew would lay the foundation for a rigorous theory of group size and within-group conflict (11, 73–75, 80, 84, 102), ultimately leading to a comprehensive theory that relates all of the major features of animal societies to their ecological contexts, genetic structures, and internal power asymmetries (47, 82).

We first briefly describe the major alternative models of reproductive skew and discuss their major predictions. We then review the results from the first wave of tests of these skew models in insect social groups and determine which skew models are the most promising overall. We emphasize that the testing of skew theory is still in its earliest stages; however, enough preliminary tests have been performed to begin sorting among the major alternative models.

## MODELS OF REPRODUCTIVE SKEW

### Transactional Models

In transactional models of reproductive skew, group members are envisioned as yielding reproduction to each other (reproductive incentives of various kinds) in return for specific benefits. There are two main transactional models of reproductive skew, the concession model and the restraint model. These two types of transactional models differ according to whether the dominant breeder, defined operationally as the individual controlling group membership, or the subordinate breeder controls the allocation of reproduction within the group. To simplify description of these models, we initially consider only two-person groups.

### Concession Models

In concession models, the dominant individual fully controls both group membership and the fraction of total group reproduction that the subordinate breeder obtains. Concession models attempt to explain the degree of skew by predicting the conditions under which the dominant breeder should yield just enough reproduction to a subordinate to make it favorable for the subordinate to stay in the group and cooperate peacefully rather than to leave the group and reproduce independently or fight to gain exclusive control of the group's resources. Minimal reproductive payments that prevent subordinates from leaving are called "staying incentives"; payments that prevent subordinates from fighting to the death for complete control of colony resources are called "peace incentives" (82).

The very first concession models for the evolution of reproductive skew analyzed how ecological constraints on solitary reproduction, genetic relatedness of potential breeders, and productivity advantages of peaceful association should influence the magnitudes of staying incentives in vertebrate and invertebrate societies (18, 19, 71, 105–107). Reeve & Ratnieks (82) extended these models by examining how relative fighting ability among group members interacts with the above factors to influence the reproductive skew via peace incentives.

We illustrate here how the basic concession model (only staying incentives are considered) is constructed from Hamilton's rule (30) and the genetic and ecological variables described in Table 1. The three parameters entering into the basic skew model for dyadic groups are (a)  $r$ , the (assumed symmetrical) genetic relatedness between the dominant and the subordinate members; (b)  $x$ , the expected solitary reproduction by a potential subordinate relative to a lone dominant (i.e.  $s/d$ ), with lower values of  $x$  indicating harsher ecological constraints on independent breeding; and (c)  $k$ , the overall reproductive output of the dyad relative to a lone dominant member (i.e.  $g/d$ ). These variables are then used in combination with Hamilton's rule to solve for the conditions under which the dominant breeder should retain the subordinate breeder or prevent it from joining (because the dominant controls group membership) and under which the subordinate breeder should stay in the group versus leave.

**TABLE 1** Variables in two-person transactional model of skew

Variable	Kind	Meaning
<i>s</i>	Ecological	Subordinate's solitary reproductive output
<i>g</i>	Ecological	Group's total reproductive output
<i>d</i>	Ecological	Lone dominant's reproductive output
<i>x</i>	Ecological	$s/d$ (subordinate's standardized output)
<i>k</i>	Ecological	$g/d$ (group's standardized output)
<i>r</i>	Genetic	Relatedness between subordinate and dominant
<i>f</i>	Social	Probability that subordinate wins a lethal fight

Hamilton's rule for deciding which of two alternative strategies will be favored by selection has the following form: Strategy *i* will be favored over strategy *j* if

$$(P_i - P_j) + r(K_i - K_j) > 0, \quad (1)$$

which is equivalent to

$$P_i + rK_i > P_j + rK_j, \quad (2)$$

where *r* is the coefficient of relatedness between the two interactants,  $P_i$  (or  $P_j$ ) is the personal reproduction associated with strategy *i* (or *j*), and  $K_i$  (or  $K_j$ ) is the other party's reproduction if strategy *i* (or *j*) is performed.

In the basic concession model, the proportion *p* of overall direct reproduction yielded by the dominant to the subordinate breeder in a stable association is that which gives the subordinate just sufficient incentive to remain in the association rather than leave and attempt to reproduce independently. By Hamilton's rule, this minimum *p* can be found by solving  $pk + r(1 - p)k = x + r$ , yielding the staying incentive *p* expressed as a fraction of total dyad output:

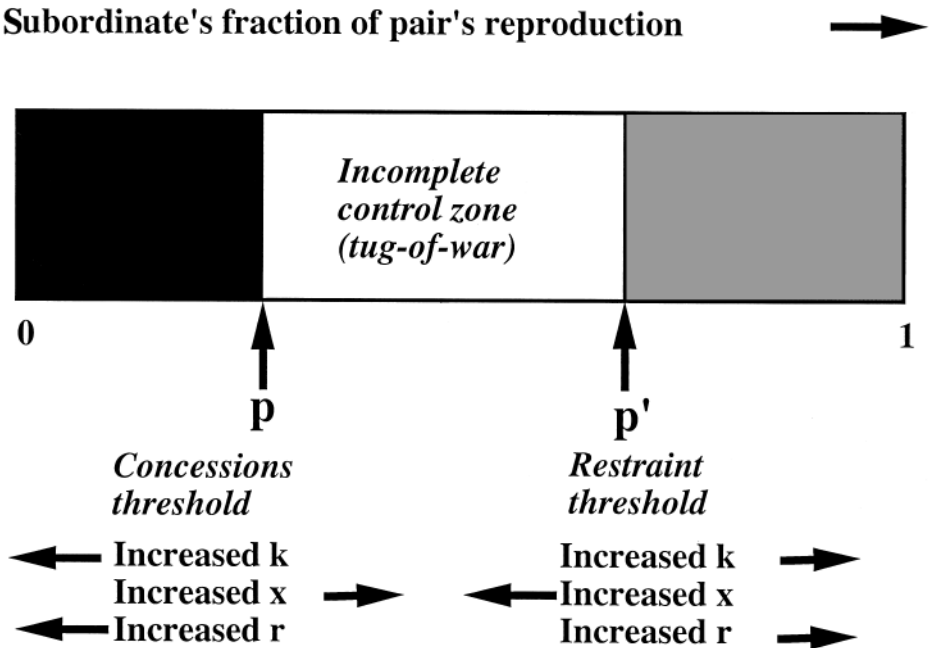
$$p = [x - r(k - 1)]/k(1 - r). \quad (3)$$

Next we must use Hamilton's rule to derive the conditions under which it pays the dominant breeder to retain the subordinate given that the latter receives its staying incentive. All of the model outcomes are shown in Table 2. If ecological constraints are strong, corresponding to the condition  $x < r(k - 1)$ , the subordinate will stay in the association with no reproduction; that is,  $p = 0$  (maximum skew). If ecological constraints are moderate, that is,  $r(k - 1) < x < (k - 1)$ , then the subordinate will receive the staying incentive given by Equation 3. The staying incentive in the concession model decreases in magnitude (meaning that the skew increases) as the relatedness *r* increases, the total group output *k* increases, and the solitary output *x* decreases (summarized in Figure 1). If ecological constraints are weak, corresponding to the condition  $x > (k - 1)$ , the subordinate member is refused by the dominant and reproduces solitarily (82; Table 2).

**TABLE 2** Evolutionary outcomes in the transactional skew models (staying incentives only)

Context	Condition	Subordinate's share	
		(Concession model)	(Restraint model)
Weak ecological constraints	$x > k - 1$	None; dominant <sup>a</sup> refuses subordinate	None; subordinate leaves voluntarily
Moderate ecological constraints	$r(k - 1) < x < k - 1$	$[x - r(k - 1)]/k(1 - r)$	1, if $x < (k - 1)/r$ ; $[(k - 1 - rx)]/k(1 - r)$ , if $x > (k - 1)/r$ (never reaches 0)
Strong ecological constraints	$x < r(k - 1)$	0	1, if $x < (k - 1)/r$ ; $[(k - 1) - rx]/k(1 - r)$ , if $x > (k - 1)/r$ (never reaches 0)

<sup>a</sup>Dominant is the individual that controls group membership.



**Figure 1** Subordinate's reproductive share under concession and restraint (transactional) models and under incomplete control (tug-of-war) models.

Thus, the general conclusions of the basic concession models are that the skew should either stay the same or increase as (a) the relatedness  $r$  between dominants and subordinates increases (because a subordinate that is more closely related to a dominant requires less direct reproduction to be favored to stay and help the dominant), (b) the probability of successful solitary reproduction by the subordinate  $x$  decreases (i.e. for stronger ecological constraints, because a subordinate has less incentive to leave); and (c) the subordinate's contribution to colony productivity  $k$  increases (because the larger this contribution, the less the subordinate must be compensated). No group forms at all if  $x > (k - 1)$ , a condition that is independent of genetic relatedness.

Reeve & Ratnieks (82) further showed that peace incentives increase (and the skew decreases) as the subordinate's relative fighting ability  $f$  increases. Peace incentives are given at any level of ecological constraints provided that  $f$  is high enough. One important prediction of this model (to which we return later) is that the dominant and subordinate will fight to the death if  $k < 1$  (i.e. the subordinate's presence actually reduces the dyad's output) and  $f > x/(1 - r)$  (i.e. the subordinate's fighting ability is sufficiently high, the ecological constraints on independent breeding are sufficiently harsh, and the relatedness is sufficiently low). Thus, the concession model makes quantitative predictions not only about the partitioning of reproduction but also about the circumstances under which groups should form or break up (through departure of the subordinate or lethal fighting), a point that is often neglected in tests of concession models.

There have been a number of recent extensions to the concession theory that are potentially quite important for interpreting skew data in social insects. We briefly summarize the most relevant new developments below.

**Dynamic Skew** The values of the reproductive outputs  $g$ ,  $s$ , and  $d$ , and thus  $x$  and  $k$ , should be viewed not as instantaneous parameters, but as cumulative expected future outputs from a specified moment in time until the breakup of the group (51, 68, 83). Likewise, the staying incentive should be viewed as the subordinate's fraction of present and future total group reproduction, which may change over time as the expected future outputs change. The importance of this forward looking view of the skew parameters is illustrated by cases in which subordinates have some nonzero probability of inheriting the nest and becoming the sole breeder in the future. When the latter is true, the subordinate's instantaneous fraction of reproduction may be quite low even though the cumulative staying incentive is predicted to be high (51, 68).

**Parent-Offspring Associations** The concession model presented above assumes that dominants and subordinates are symmetrically related to each other's offspring. This is not the case when the dominant female is the mother of the subordinate (e.g. a worker). Reeve & Keller (77) showed that the asymmetry in relatedness occurring in mother-daughter associations versus sibling associations should tend to increase the degree of skew in the former, because daughters will

often be neutral about whether siblings or their own offspring are produced (but mothers will always prefer to produce sons and daughters over grandchildren). In hymenopteran societies, there is an additional twist: A subordinate daughter of a singly mated mother queen will prefer that the mother produce female offspring but will prefer to produce the males herself because she is three-fourths related to sisters but only one-fourth related to brothers (compared with a relatedness of one-half to sons and daughters). Thus, the worker and queen can be in conflict over male production, and it is conceivable that there will be a split skew, that is, a complete skew for female offspring but a partial skew for male offspring when the subordinate daughter demands a staying incentive. A subordinate daughter should demand a fraction of the female production only if the mother queen is multiply mated.

***The Bidding Game*** The basic concession model has recently been expanded to encompass the case in which dominants in two or more colonies compete for the services of a helping subordinate [the “bidding game” (72)]. In such a case, dominant breeder-subordinate relatedness is not predicted to affect the reproductive skew, and (in further contrast to predictions of the basic concession models) the skew is predicted to decrease as the subordinate’s contribution to colony productivity increases. The latter effect arises because a greater contribution by the subordinate makes a dominant member willing to “bid” more for the services of that subordinate, in the form of an increased staying incentive. In a bidding game, we expect frequent nest switching by subordinates and low skews.

***Partner Preferences*** Reeve (72) showed that dominants should prefer relatives as subordinates, given a choice between relatives and nonrelatives in the basic concession model (subordinates are neutral about the relatedness of the dominant member if they receive a positive staying incentive). However, in the bidding game, both dominants and subordinates are predicted to be neutral about the relatedness of their partner, and a high frequency of associations of nonrelatives should occur; that is, relatedness is expected to be highly variable (72).

***Group Size*** Johnstone et al (42) extended the two-person concession model to the difficult three-person case. The central predictions are unchanged, but the addition of a second subordinate does modify some predictions. For example, the condition describing the breakup of the group no longer is independent of relatedness.

Recently, Reeve & Emlen (74) developed a concession model of reproductive partitioning and group size for  $N$ -person groups when (a) expected group output is a concave (decelerating) function  $g(N)$  of the number  $N$  of group members and (b) each of the  $(N - 1)$ -equivalent subordinates receives a staying incentive. The model focuses especially on “saturated” groups, that is, groups that have grown in size just up to the point where subsequent joining by subordinates is no longer beneficial either to the subordinates (in parent-offspring groups) or to the dominant breeder (in symmetric-relatedness groups). Decreased expected

output for solitary breeding  $s$  increases the saturated-group size and decreases the staying incentive in saturated groups. Increased relatedness decreases both the saturated-group size and the staying incentive in saturated groups. However, in saturated groups with symmetric relatedness, an individual subordinate's staying incentive converges to  $1 - [g(N^* - 1)/g(N^*)]$ , where  $N^*$  is the size of a saturated group, provided that relatedness is zero or that the  $g(N)$  function near the saturated-group size  $N^*$  is approximately linear. Thus, staying incentives can be insensitive to relatedness in saturated groups (especially relatively large saturated groups), although the dominant breeder's total fraction of reproduction (total skew) will be more sensitive.

If group size  $N$  is held constant, the staying incentive stays the same or increases as the ratio of group output at size  $N$  to group output at size  $N - 1$  decreases (which is like  $k$  decreasing in the basic concession model), as the solitary output increases (which is like  $x$  increasing in the basic concession model), and as  $r$  decreases (again just as in the basic concession model). However, the predictions become more complex if staying incentives in differently sized groups are compared, and these predictions depend on whether the compared groups are saturated or unsaturated or a mix of both. When there is substantial variation in group size, it is essential that field workers account for this variation properly in light of the  $N$ -person models.

The predicted ordering for saturated-group size in the  $N$ -person model is as follows: parent–full-sibling offspring groups = groups of nonrelatives > groups of symmetrically related relatives. Strikingly, stable groups of nonrelatives can form for concave  $g(N)$  functions (with per capita output declining with increasing group size) in the  $N$ -person concession model but not in previous models of group size with group entry controlled by group members and the absence of skew manipulation by the dominant (29, 36, 74). Stable groups of nonrelatives can form for concave  $g(N)$  functions in transactional-skew theory because dominants in effect steal reproduction from subordinates in such groups but allow just enough reproduction for subordinates to be favored to stay. Another difference between the  $N$ -person concession model and the controlled-entry group size models without skew manipulation is that the former predicts a negative relationship and the latter predict a positive relationship between relatedness and group size. A final prediction of the  $N$ -person concession model is that symmetrical-relatedness groups should tend to break up by threatened ejections of subordinates by dominants, whereas parent-offspring groups should tend to break up via unforced departures by subordinates.

**Reproductive Skew and Caste Manipulation** Keller & Reeve (47) suggested that, in social insects in which at least some workers are reared by the queen, the queen may affect worker development so as to increase her reproductive skew (see reference 9 for a discussion of conflict over caste determination). For example, the queen might effectively reduce the worker's relative solitary success  $x$  or its fighting ability  $f$  by restricting the amount of food the worker receives as a larva. Crespi & Ragsdale (14) recently modeled this situation and concluded that such



manipulation will always lead to complete skew. However, their model didn't allow for a trade-off between reduction in solitary-breeding success and reduction in the worker's contribution to the group; for example, smaller workers may enable complete skew but they also may be less effective as helpers. Moreover, dominants may benefit from having their helping workers retain high reproductive potential, if those workers will later become replacement breeders or disperse to breed upon the dominant breeder's death. Finally, opportunities for such extreme manipulation will be limited between queens in multiqueen societies, because the latter will have had little or no chance to influence the other's development, and any attempt at such manipulation in the adult stage might be easily thwarted by simply leaving the group. Thus, the prediction that skew will always be complete is overstated.

### Restraint Models

In the concession models, the dominant breeder is assumed to control both group membership and the distribution of reproduction within the group. Johnstone & Cant (41) recently developed an alternative transactional model of skew based on the assumption that the dominant controls group membership but the subordinate fully controls the reproductive shares within the group. This model is called a "restraint" model because in it the subordinate captures the largest share of reproduction that the dominant will tolerate before ejecting the subordinate; that is, the subordinate must restrain itself from being any more selfish lest it be forced to leave the group. Thus, the subordinate's share, which is essentially a nonejection incentive given to the dominant, is higher in the restraint model than in the concession model (Figure 1).

The restraint model is solved by applying Hamilton's rule to the dominant's decision to retain versus eject the subordinate and then solving for the subordinate's share  $p'$  at which it just pays the dominant to retain the subordinate. Hamilton's rule is then applied to the subordinate's decision to stay vs leave, given that it will receive the fraction  $p'$ . The outcomes are shown in Table 2, using the same ecological and genetic variables as used in the concession model. If ecological constraints are strong, corresponding to the condition  $x < r(k - 1)$ , and if  $x$  is sufficiently small, the subordinate will stay in the group and receive all of the reproduction ( $p' = 1$ ); otherwise, the subordinate provides the dominant with a nonejection incentive. Importantly, the subordinate's share of reproduction never falls to zero (complete skew) in the restraint model. If ecological constraints are moderate, that is,  $r(k - 1) < x < (k - 1)$ , then the subordinate again will stay in the group and receive all of the reproduction ( $p' = 1$ ) if  $x$  is sufficiently small; otherwise, the subordinate provides the dominant with a nonejection incentive. Under weak ecological constraints [ $x > (k - 1)$ ], the subordinate leaves the association voluntarily. Thus, the restraint model makes the prediction that groups will break up via unforced departures by subordinates, whereas the concession model predicts that they will break up because the dominant has taken some action to remove subordinates (Table 2).

The dominant breeder's nonejection incentive depends on  $x$ ,  $k$ , and  $r$  in much the same way as does the staying incentive in the concession model (and the verbal logic describing these dependencies is the same). However, this means that the subordinate's share of reproduction depends on  $x$ ,  $k$ , and  $r$  in ways exactly opposite to the subordinate's reproductive share in the concession model. The subordinate's share in the restraint model decreases in magnitude (meaning that the skew increases) as the relatedness  $r$  decreases, the total group output  $k$  decreases, and the solitary output  $x$  increases (summarized in Figure 1). Thus, the restraint model makes predictions that are quite distinct from those of the concession model. Indeed, for sufficiently high relatedness (or high  $k$  or low  $x$ ), the subordinate in a restraint model is predicted to out-reproduce the dominant.

## Tug-of-War Models

The transactional (concession and restraint) models explain reproductive sharing as the offering of reproductive incentives by dominants to subordinates or vice versa, and both models assume that either the dominant or the subordinate is fully in control of the distribution of reproduction. Reeve et al (75) developed a completely different model for the evolution of reproductive sharing, in which both dominants and subordinates have only limited control over the allocation of reproduction within groups, and reproductive sharing simply reflects each group member's inability to profitably monopolize the group's reproduction. In their tug-of-war models [or incomplete control or "compromise" models (40)], dominants and subordinates have only limited control over the allocation of reproduction and must expend effort to increase their shares of the total group output. These selfish efforts come at the expense of total group output. This model formalizes what seems to be the most widespread view of the evolutionary significance of reproductive sharing.

The tug-of-war models predict that, when the relatedness between dominant and subordinate is symmetrical, (a) the subordinate's fraction of reproduction either increases with or is insensitive to the subordinate's genetic relatedness  $r$  to the dominant, (b) the subordinate's share of reproduction must exceed that in the concession-skew model (otherwise the group will break apart), and (c) ecological factors affecting solitary-breeding success do not directly affect the subordinate's share of reproduction (as they do in the transactional models). In parent-offspring groups, the tug-of-war model predicts no reproduction by the subordinate offspring regardless of group size for groups containing any mixture of unrelated and full-sibling subordinates. Thus, both transactional (concession and restraint) and tug-of-war models predict higher skews in parent-offspring groups than in groups of symmetrically related individuals.

The tug-of-war model can be seen as predicting a reproductive skew that is intermediate between those predicted by the concession and restraint models. In terms of Figure 1, the zone in which a tug-of-war model determines the subordinate's share is the region between the subordinate's share of reproduction in the

**TABLE 3** Predictions of the major skew and aggression models. The effect of each parameter assumes that other parameters and the group size are held constant.

Variable	Skew model's predicted association of variable with skew			
	Concessions	Bidding game <sup>a</sup>	Restraint	Tug-of-war
<i>x</i>	Negative	None	Positive	None
<i>k</i>	Positive	Negative	Negative	None
<i>r</i>	Positive	None	Negative	None or negative
Aggression model's predicted association between aggression and skew				
	<b>Transactional</b>		<b>Pure tug-of war</b>	
	Positive		Negative	

<sup>a</sup>The bidding game model also predicts switching of subordinates between nests and lower skews than in concessions models.

concession model (the lower threshold in Figure 1) and that in the restraint model (the upper threshold in Figure 1). Figure 1 shows that the concession, restraint, and tug-of-war models, while distinct, can be viewed as describing solution subspaces for a more general model of reproductive skew, and, indeed, Johnstone (40) has shown how these models can be stitched together into such a synthetic model. Nevertheless, we treat these models as distinct and testable alternatives for explaining reproductive skew in a given kind of group, because they make different families of predictions about the relationships between the skew in one kind of group and the ecological and genetic variables pertaining to that group (Table 3).

## Reproductive Skew and Within-Group Aggression

A widespread current misconception is that transactional models predict the absence of within-group conflict because of the focus on peaceful transfers of reproduction (13, 14, 37). On the contrary, one of the exciting features of transactional models is that they can be used to predict variation in the level of intragroup conflict, from conflict-free to conflict-ridden societies (11, 73, 80, 82).

A number of quantitative models now exist that predict the relationship between reproductive skew and the amount of within-group conflict (11, 73, 75, 78, 80, 82). We do not review these models here (see 73), but briefly describe a model that is general, simple, and has an intimate connection to transactional theories of skew. This window-of-selfishness model predicts that the frequency of aggression (or other forms of conflict) within groups will increase as the gap between the lower concession threshold and the upper restraint threshold in Figure 1 increases (73, 78). This gap is the "window of selfishness," which describes the scope for conflict within the group, that is, the maximum amount by which one group member can increase its reproductive share (e.g. in a tug-of-war) without causing group dissolution. In other words, the window-of-selfishness model predicts that the

degree of conflict will be circumscribed by the magnitudes of the reproductive payments required to keep the subordinate from leaving (or fighting) and the dominant from ejecting the subordinate—this is what makes the model transactional in nature. When the window is wider, one group member (e.g. the dominant one in concession models) can forcibly take a greater fraction of reproduction from the other without losing the cooperation of the latter.

Thus, in the two-person skew model, the frequency of aggression is predicted to rise as ecological constraints become harsher ( $x$  decreases), the subordinate's contribution  $k$  increases, and the relatedness  $r$  increases, that is, as the reproductive skew increases (73). The window-of-selfishness also has been derived for the  $N$ -person concession model, which predicts that aggression should be minimal in saturated groups (because the two thresholds in Figure 1 have moved together to produce a zero-width window of selfishness) and should increase as group size falls below the saturation size (73). In the bidding game, the window of selfishness also has zero width, as in the saturated-group  $N$ -person concession model (72).

The window-of-selfishness model will fail if the subordinate's reproductive share never approaches the lower or upper thresholds in Figure 1 or if most aggression does not reflect selfish attempts to enhance an individual's reproductive share. For example, if most aggression instead reflects threats to leave, fight, or eject (all occurring in the vicinity of the lower and upper thresholds in Figure 1), then all of the window-of-selfishness predictions are reversed, because aggression then should increase as the two thresholds move closer together (101).

The pure tug-of-war model, unbounded by required reproductive incentives, makes quite different predictions about the level of conflict within groups, measured by the selfish effort each group member invests in the tug-of-war (75). The model solutions predict that the subordinate's selfish effort (e.g. aggression) should exceed the dominant's selfish effort and that the total selfish effort will be negatively related to the reproductive skew. Moreover, the total aggression will increase as the competitive abilities of group members become more closely matched. In transactional models, increasing fighting ability of the subordinate relative to the dominant member can either increase or decrease the window of selfishness, depending on the ecological conditions.

## Summary of Theoretical Predictions

In summary, each of the existing alternative skew models generates a diverse family of predictions (and also has different testable assumptions; Table 3). Individual predictions may be shared by two or more models (e.g. increasing skew as relatedness decreases in the restraint and some versions of the tug-of-war models), but the families of predictions from alternative models are quite distinct. Clearly, tests of skew models should involve as many predictions as possible within each distinct family of predictions, because testing only a single prediction, such as the relationship between skew and relatedness, will often be only weakly informative.

Moreover, predictions about a relationship between skew and one variable may depend on the values of other variables. For example, the concession model prediction that skew will increase with increasing relatedness assumes that the social group is under moderate ecological constraints when staying incentives are given; under strong ecological constraints, the skew is complete, and no such relationship is expected. Thus, tests of skew theory ideally should examine all of the ecological and genetic parameters pertaining to the society. Empirical tests of the alternative models' entire families of predictions should permit rapid progress in assessing which skew models are most applicable generally and in specific cases.

In assessing evidence for the alternative models of reproductive skew, we focus primarily on predictions of the effect on skew of relative solitary-breeding success  $x$ , relative group output  $k$ , and relatedness  $r$ . The basic concession model predicts that skew should tend to increase with increases in  $k$  and  $r$  and decrease with increases in  $x$ . The restraint model predicts exactly the opposite. The tug-of-war model predicts that  $x$  and  $k$  will not affect skew and that increasing  $r$  will either not affect skew or cause it to decrease. The bidding game (a special kind of concession model) predicts that relatedness will not affect skew, subordinates will frequently switch between groups, and the skew will be low (Table 3). We draw on the other predictions of the skew models (e.g. regarding group size or aggression) as needed, according to the kind of data gathered in each study.

## TESTS OF REPRODUCTIVE-SKEW THEORY IN SMALL INSECT SOCIETIES

To date, most studies that have explicitly tested skew theory have focused on small colonies of social insects, in which the assumption of complete control of reproductive shares has appeared reasonable. We review this evidence below (roughly in descending order of amount of evidence) and later review how the characteristics of even large-colony social insects can be illuminated by skew theories.

### Polistine Wasps

Cooperative associations of social-wasp queens are ideal systems for testing theories of reproductive skew (71). In social wasps of the genus *Polistes*, multiple queens often cooperate in founding spring nests after overwintering (58, 71, 108). A linear dominance hierarchy develops among these foundresses, and the most dominant foundress (alpha) usually lays most but not all of the eggs. In the temperate species *Polistes fuscatus*, the first brood develops into early females, some of which become workers (which sometime reproduce as replacement queens), but many or most of which leave the nest to become foundresses the following year (81). Later broods develop into males and late females, the latter also becoming part of next year's pool of foundresses (58, 71, 108).

In an early comparative analysis, Reeve (71) found that polistine societies tend to exhibit one of two syndromes: (a) high skews and high levels of foundress aggression or (b) low skews and low levels of foundress aggression (but with frequent differential oophagy and egg replacement). This trend supports the transactional theory of within-group conflict, which predicts that low skews will be associated with low levels of aggression.

According to the concession skew model, a subordinate foundress should require a smaller staying incentive (i.e. the reproductive skew should be larger), as (a) the colony's overall productivity increases, (b) the second-ranked subordinate (beta)'s genetic relatedness to alpha increases, and (c) beta's reproductive output, if it were to solitarily found a new nest, decreases. Reeve et al (83) tested and found strong support for all of these predictions with a genetic (microsatellite) analysis of reproductive partitioning within 24 multiple-foundress *P. fuscatus* colonies from the same population. Reproductive skew was significantly higher in associations of full sisters than in associations of cousins and significantly increased (relatedness controlled statistically) as nest size, measured as total number of brood cells, increased. Group size was not a confounding variable because all of the predictions also held when only two-foundress groups were included in analyses.

In *Polistes*, the likely major benefit of nest founding in groups is survival insurance, that is, increased protection from chance loss of all colony adults before the first workers emerge (57, 71, 80). Reeve et al (83), using a forward looking, dynamic concession model, showed that the survivorship insurance model predicts that reproductive skew should increase over the course of the founding phase, because the survival of a newly established solitary foundress's nest declines relative to the survival of an established multifounded nest as worker emergence approaches. As predicted, the reproductive skew increased as the colony cycle advanced. Part of the increase in skew over time could reflect the decreasing probability that a female offspring will become a worker over time (i.e. an increasing value of female offspring), but this is unlikely to completely explain this trend: It appears that half or more of the early females disperse as reproductives (i.e. the value of a female less than doubles later on), whereas the subordinate's share of the brood decreases by a factor of 7 between production of early and late brood (moreover, the reproductive value of the earlier females will be increased as the chance increases that the colony will be destroyed by predators before later females emerge). Increases in skew after colony initiation also are strongly suggested by the observed temporal changes in skew in foundress associations of *Polistes annularis* (65) and *Polistes bellicosus* (21).

Aggression between alpha and beta was higher on later nests of *P. fuscatus* (as also found in reference 26) and also on more productive nests, the latter also having higher reproductive skew. Thus, the results indicate that higher aggression is associated with higher skew, as predicted by the transactional model of within-group conflict. The opposite relationship is predicted by tug-of-war models (Table 3), because increasing subordinate competitive efficiency both decreases the skew and raises the evolutionarily stable levels of aggression for alpha and beta (75).

The increase in skew over time sheds new light on the significance of foundress responses to experimental egg removal in the study species (79, 89). Removal of female- and male-destined eggs late in the founding phase increased alpha's aggression toward beta (the second-ranked subordinate) and especially beta's aggression toward alpha, but removal of female-destined eggs early in the founding phase caused a significant decrease in alpha's aggression and no change in beta's aggression. The large drop in alpha's aggression when valuable early-female eggs are removed (i.e. when a substantial fraction of the removed eggs are betas) strongly supports the concession model interpretation that alpha is unwilling to engage in aggressive egg-laying competition when the beta is at greatest risk of losing her minimal staying incentive (suppression of alpha's aggression is associated with a lack of increase in beta's aggression). Importantly, the concession model also provides an elegant explanation for the paradoxical finding that "... in early foundress associations, queens frequently exhibit behavior characteristic of subordinates in mature hierarchies" (24). The skew data indicated that paradoxical dominance reversal occurs at precisely the time when the alpha is peacefully conceding a staying incentive to the beta. Late in the founding phase, when beta's staying incentive is only ~7%, alpha and beta appear to openly engage in aggressive competition to replace the removed eggs in newly emptied cells. Egg removal at this stage stimulates especially large increases in beta's aggression not only because of the enhanced egg-laying competition with an aggressively competing alpha, but also because beta may be retaliating for losing her (albeit small) staying incentive (79).

In contrast to the above skew patterns for *P. fuscatus*, skews in *P. bellicosus* foundress associations are high overall, higher in larger groups, and inconsistently (negatively or not) associated with the relatedness between cofoundresses; moreover, foundress aggression was higher in lower-skew groups (which tended to be smaller) (21). Superficially, these data appear to support the tug-of-war model, and, indeed, Field et al (21) interpreted these observations as evidence against the concession model.

However, these results may be confounded by group size (73, 83) and are compatible with the *N*-person concession model if most (the larger) of the foundress groups in *P. bellicosus* (unlike those in *P. fuscatus*) were close to saturation. Indeed, 79% of the *P. bellicosus* associations, but only 40% of *P. fuscatus* associations, consisted of more than two foundresses. As group size increases for saturated groups, the staying incentive tends to decrease despite the fact that the window of selfishness remains uniformly zero (variation in the saturation size among groups could arise from nest site variation in the group output function). Thus, low or no aggression can be present in high-skew colonies if the latter are saturated. It follows that, if only the smallest groups are unsaturated (and thus have a positive window of selfishness), one would expect higher skew to be associated with both larger group size and decreasing aggression, as was observed (21).

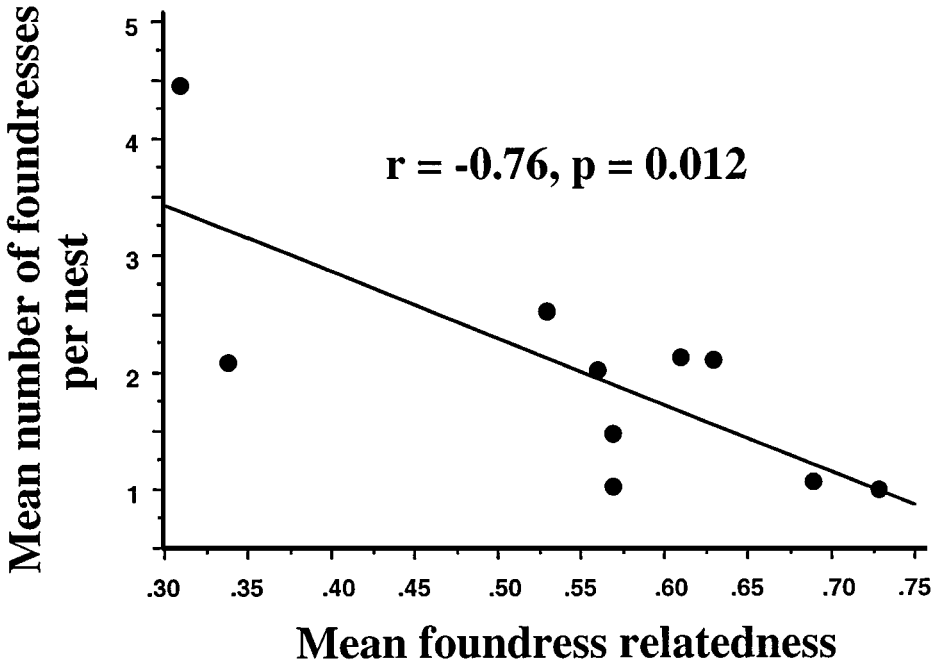
The latter interpretation of the Field et al (21) results generates a testable prediction: If it is true that most foundress groups in their study population were saturated, then the overall level of aggression within these groups should have

been very low. Indeed, the authors noted that overall level of foundress aggression was very low compared with that of other species (21), exactly as predicted by the  $N$ -person model. It is plausible that groups in this study population were especially likely to be near saturation, given that the mean number of foundresses is higher than that typically seen in *Polistes* populations exhibiting high levels of intracolony aggression. A crucial test of this idea would be to examine whether groups with some foundresses removed exhibit higher aggression than intact groups, since such removal should always increase the distance from saturation and thus the width of the window of selfishness (73).

The  $N$ -person concession and conflict models are supported by other data from polistine wasps. Removal of low-ranked (principally foraging) workers from colonies of *P. fuscatus* causes a significant increase in aggression between the remaining high-ranked females and the dominant foundress (27). Because removal of workers caused an increase in the distance from the saturated group size (even if they were unsaturated to begin with), this result supports the prediction from the  $N$ -person model that conflict should increase in frequency as the distance from saturation increases. Recent evidence also indicates that aggression between *P. fuscatus* foundresses declines just after the workers emerge (92). This result also is predicted by the  $N$ -person model, because the emergence of workers must decrease the distance from saturation and thus reduce the window of selfishness for dominant and subordinate foundresses (73). Moreover, since the saturation group size for foundresses is less than that for workers according to the  $N$ -person model (74), the  $N$ -person model predicts that subordinate foundresses should tend to disappear after worker emergence (because of their reduced contribution), which is commonly observed (reviewed in 71). The disappearing foundresses are likely pursuing new reproductive options, such as nest adoption or usurpation (25, 57). In addition, the  $N$ -person concession model's prediction of an inverse relationship between cofoundress relatedness and mean group size is observed across populations in which both were measured (Figure 2). (Note that the prediction of an overall negative relationship does not assume that most groups within each population are saturated or even that different populations have the same frequency of saturation—only that at least some colonies are saturated in some of the populations.) However, this relationship by itself is not particularly strong evidence for the  $N$ -person model because it could be generated in a variety of ways. Also in support of the  $N$ -person model is the finding that foundress groups form more frequently when solitary foundresses have lowered survival probability (71).

Finally, the recent discovery that stable associations of unrelated foundresses often form in *Polistes dominulus* (67) supports transactional models of group size as opposed to models of group size without skew manipulation, because the latter predict that such nonrelatives should never form when group members control group membership and the  $g(N)$  function is concave [which appears to be generally true for *Polistes* (71)]. The similarly high skews in both related and unrelated foundress groups are predicted by concession models of skew under high ecological





**Figure 2** Relationship between mean foundress group size and mean cofoundress relatedness measured for each of 10 populations of *Polistes* wasps [*P. annularis*, *P. bellicosus*, *P. carolinus*, *P. exclamans* (Rio Grande and Houston), *P. instabilis*, *P. metricus*, *P. versicolor* (38), *P. jadvigae* (103), and *P. fuscatus* (80, 83)]. Mean cofoundress relatedness was measured as mean relatedness of fall nestmates under the previously supported assumption that this approximately equals the relatedness of spring foundresses (38); the latter was measured directly for *P. fuscatus* (83).

constraints [i.e. as  $x/(k - 1)$  approaches 0; see Table 2], so it is crucial to know the ecological conditions in this population. A high probability of nest inheritance may also contribute to the uniformly high skews in this species (67). A recent analysis of patterns of cofoundress aggression in *P. dominulus* strongly supports the transactional and not the tug-of-war model of within-group conflict (101).

It is not widely recognized that concession models (but not restraint models nor tug-of-war models) predict that subordinates that share reproduction with dominants should have inclusive fitnesses roughly equivalent to the inclusive fitnesses of solitary foundresses, because the dominant is predicted to concede just enough reproduction to equalize these two quantities. This prediction may explain why applications of Hamilton's rule to the subordinate joining decision have generally revealed that the inclusive fitness payoffs for solitary founding are close to (only slightly above or below) the payoffs for joining as a subordinate (54a, 57, 58, 66).

## Carpenter Bees (Xylocopini and Ceratinini)

Hogendoorn & Velthuis (37) recently examined how well concession skew theory can explain variations in skew within and between species of carpenter bees (Xylocopini and Ceratinini), which tend to have only two group members (often a mother and a daughter). In *Xylocopa pubescens*, the authors calculated the theoretical skew from empirical data both for subordinates that are old females (which were shown to have lower expected nest-founding success than do younger females) and for subordinates that are young females. The observed complete skew for old subordinate females matched the theoretical prediction, but skews also were complete for young subordinate females, which were observed to share in reproduction. However, these estimated skew parameters did not account for the especially high frequency with which young subordinate females are known to later supersede the older dominant females [i.e. the skew parameters were not “forward looking” in time (see above)]. Incorporating this effect as in inheritance models of reproductive skew (51, 68) would likely account for the complete skew for younger female subordinates.

The concession model is supported by some but not all of the data. In *Ceratina* species, subordinates typically obtain a share of the reproduction, whereas in *Xylocopa* species, skew is typically complete. Nest material appears to be less limiting in the former species, supporting the concession model prediction that skew should tend to decrease as  $x$  increases. In *X. pubescens*, the concession model correctly predicts that groups should not form in the spring, when the presence of a guard does not increase the output of a dominant member [ $x > (k - 1) = 0$ ]. The positive association between skew and aggression supports the transactional (73) and not the pure tug-of-war model of intragroup conflict (75).

However, the failure of colony productivity  $k$  to predict variation in skew within a population of *Ceratina okinawana* is more consistent with a tug-of-war model. In addition, relatedness by itself did not predict variation in skew in *Ceratina japonica*: Skew was similar in semisocial (same-generation) and eusocial (dominant-mother–subordinate-daughter) groups, but the highest skews were in reversed eusocial (dominant-daughter–subordinate-mother) groups despite the lower relatedness of the subordinate (the mother) to the offspring of the dominant (the mother’s grand-offspring) in the latter groups. However, the reversed eusocial groups probably occur later in the season than do eusocial and semisocial groups, so the concession model may still possibly account for the pattern of skew if ecological constraints on solitary breeding become harsher as the season progresses (a testable prediction). In addition, the patterns of skew in carpenter bees suggest that skew theory for mother-daughter associations should be expanded to account for changes in reproductive value in females as they age—old mothers may be less fecund as the season progresses, accounting for reversals in dominance and high skews in groups in which old females become subordinates. In summary, the data presented suggest partial support for the concession model and partial support for the tug-of-war model of skew.

## Halictid Bees

Richards et al (86) found ecologically driven variation in skew within dominant-parent-subordinate-offspring groups of the halictid bee *Halictus ligatus*. In a rainy year with high rates of nest failure (relatively low  $x$ ), the queen's reproductive skew was significantly higher than the reproductive skew in a drier year with lower rates of nest failure (higher  $x$ ), as predicted by the concession model. Interestingly, in the low-skew year, the workers (which frequently are mated) produced many of the reproductive-female offspring. This is expected under the concession model only if the queen had effectively mated with two or more males, which was what the authors found (86).

Multiple-foundress associations do occur in halictid bees (55), but relatively few studies have examined the relationship between reproductive skew and foundress relatedness or ecological variables in such associations. In one of the few studies, Richards & Packer (85) found that foundresses in *H. ligatus* have very low relatedness and that reproduction is shared extensively (worker-worker relatedness is very low, and subordinates have a high chance relative to dominants of surviving to the postworker phase of the colony cycle), although the skew is not likely to be completely equitable. These data appear most consistent with the concession model, given that ecological conditions appear to be mild (only 12% of colonies are multiply founded and even workers reproduce in singly founded parent-offspring groups). Aggression has been seen between foundresses, but primarily in the context of permanent and deadly ejection from the nest, which is suggestive of the transactional prediction that lethal fighting will be most common when subordinates are least related to the dominant (see above). Finally, per capita productivity appears to decline with an increasing number of foundresses, so the coexistence of several unrelated foundresses is more consistent with a group size model that assumes skew manipulation than with group size models without the latter (74).

The tendency for eusociality in halictid bees to revert to a solitary condition at high altitudes or latitudes (84) is readily accommodated by the transactional model of group breakup: At high altitudes or latitudes, the short warm season means that even the first group of emerging "workers" would do better to overwinter as next year's foundresses than to stay and help as workers, that is,  $x > (k - 1)$  because  $x$  is so high and  $k$  is so low (Table 2).

## Allodapine Bees

Studies of Australian allodapine bees (93) suggest that large colony size and large skew in this group are a derived state that has coincided with increased predation pressures favoring larger associations of nest-guarding females (including foundress associations). Skew was assessed indirectly as the frequency of small females specialized for the worker role and apparently with low reproductive potential. If genetic studies confirm this expectation, these data will be most consistent with a concession model because increased ecological constraints (low  $x$  or high  $k$ )

are associated with larger group size and mean lower reproductive shares for individual subordinates (within-group relatedness tends to be high, i.e., 0.50–0.75). In the species with especially large group sizes, the group output function is exceptionally convex (i.e. there is increasing per-capita reproduction) up to three to five individuals, before becoming concave (94), in support of the  $N$ -person skew model predictions (74). Finer resolution of these predictions awaits detailed analysis of within-population variation in group size and skew.

Interestingly, there is substantial evidence in allodapines that supports the partner choice models of reproductive skew (72). Females prefer to group with relatives when given a choice between relatives and nonrelatives but will nest with nonrelatives if no relatives are available (e.g. in recently burnt areas), provided that ecological constraints are harsh (high  $k$  or low  $x$ ) (if ecological conditions are mild, the model predicts that dominants will be less willing to accept nonrelatives). Indeed, ecological constraints appear harsh, because two-female groups in these allodapines have more than twice the output of solitary females (93).

## Communal Bees and Wasps

In communal wasps and bees, unrelated females (often a large number) share nests with other females typically with low or zero reproductive skew, with each female independently ovipositing and caring for brood (15, 52, 53, 55, 60). For example, recent genetic and observational data on the communal bees *Perdita texana* and *Andrena jacobii* showed that nestmate females are only distantly related and appear to contribute relatively equally to total group reproduction regardless of group size (15, 60). These data support the concession model.

In at least some communal bees, the function  $g(N)$  relating group output to group number is linear (53), allowing immediate quantitative deductions about group size and reproductive skew from the  $N$ -person concession model. Each individual's share of reproduction in this model is exactly  $1 - [g(N-1)/g(N)]$  for unrelated individuals (74), which reduces to just  $1/N$  if the group output function is of the linear form  $cN$ , where  $c$  is a constant. Moreover, there is no upper size at which groups saturate.

Thus, the observed zero skew and large group sizes are well predicted by the concession but not the other models. In addition, the absence of dominance and low levels of aggression follow from the transactional model of intragroup aggression (73). [Note that transactional theory predicts when individuals will behave as dominants, which is often misunderstood. For example, Crespi & Ragsdale (14) mistakenly asserted that dominance is assumed by transactional models, when all that is assumed is that one group member exists that conceivably could control reproductive shares. Whether dominance behavior actually evolves is a prediction, not an assumption, of transactional theory. Below, we also show that even the assumption of complete control of reproductive shares by a single individual is not required for transactional skew models to apply.]

## Burying Beetles

Female burying beetles (*Nicrophorus* sp.) often cooperate in raising young on buried carcasses, and they may benefit from these associations by being able to out-compete fly larvae that are also present on the carcasses (16, 17, 88, 94, 95). These associations likely consist of nonrelatives, and reproduction is skewed in favor of the dominant female, but the reproductive skew decreases as the size of a shared carcass increases. The latter result is most consistent with the restraint transaction model if a large carcass reflects a higher  $k$ , that is, a higher contribution by the subordinate. In support of the latter interpretation, associations are less common on small than on large carcasses [in the transaction model, grouping is favored only if  $x < (k - 1)$ ] (16, 17, 88). However, aggression is less common on large carcasses than on small carcasses (17), which weakens a transactional interpretation unless aggression on small carcasses reflects primarily eviction rather than attempted enhancement of reproductive shares within stable pairs.

Robertson et al (88) alternatively suggest that the data support what is essentially a concession model but that on large carcasses the dominant's ability to control skew lessens; therefore, these authors propose a combination of the concession and tug-of-war models. However, a tug-of-war model predicts higher aggression when skew is lower, whereas aggression appears lower on larger carcasses where skew is lower (17). Reeve (72, 73) earlier proposed that these data support the bidding-game model, but it is doubtful whether subordinates can readily switch from one dominant to another (17).

## Founding Colonies of Ants

In many ant species, unrelated queens cooperate to initiate a new colony (4, 43, 97). These "pleometrotic" associations form when there are high ecological constraints on solitary breeding (low  $x$ ; there is typically a high predation risk while queens search for suitable nesting sites and dig burrows), and there are usually high benefits of grouping (high  $k$ ) as manifested by the greater productivity and survival of multiple-female associations. Typically, all queens peacefully contribute to reproduction, although it is possible that some queens produce more eggs and/or workers before the eclosion of the first workers (3, 4, 44, 87, 90).

The low initial skew is apparently in accord with the concession model, given the zero relatedness between founding queens, but the strong ecological constraints (low  $x$  and high  $k$ ), should lead to nonequitable reproductive sharing among group members. (In addition, ecological constraints should become even more severe over time, because the energy reserves of queens decrease as they feed the larvae, thus rapidly hampering their ability to initiate a new colony independently.) Even more importantly, the first brood consists of sterile workers, so it may not be obvious how the skew models apply to this early partitioning of a brood among foundresses (82).

The proper way to apply transactional-skew (e.g. concession) theory is to adopt a forward looking view of the ecological parameters and the staying incentive. An interesting feature of cooperative foundations of ants is that only a single queen generally survives worker emergence (4, 91). Hence, a single queen will inherit the colony and monopolize production of new queens and males, with the effect that the skew is complete from worker emergence onward. This seems to contradict transactional models and raises the question of why queens peacefully cooperate until worker eclosion, given that all but one will ultimately have a zero-inclusive fitness. The answer is that, at the time when queens decide whether to nest alone or in a group, the expected future inclusive fitness for group nesting is likely higher. That is,  $x < (k - 1)$  when expected future reproduction is computed, owing to higher future survival of colonies founded multiply rather than solitarily. Queens would be favored to stay in such groups even if their probability of becoming the “winning” queen is only  $x/k$  (Table 2). Under such conditions, the queens benefit from cooperating and not fighting lethally, at least until the eclosion of the first workers, at which time  $k$  likely becomes  $< 1$  (as the result of workers taking over colony tasks previously assumed by queens; see below).

Note that multiple-queen associations will be stable only if there is at least some uncertainty about which queen will survive until the first workers eclose. Interestingly, experimental studies in fire ants showed that there was a tendency for larger-headed queens (as well as the queen losing less weight during the founding period) to survive more frequently than smaller queens losing more weight, but the association between these phenotypic attributes and probability of survival was weak (2). This suggests that there may be a weak dominance hierarchy among queens, with all queens having a nonzero chance of survival. Thus, cooperation among unrelated founding queens makes sense in light of the concession model if the probability of becoming the lone surviving queen is viewed as the staying incentive. This interpretation nicely explains why cofounding ant queens cooperate in an apparently peaceful manner until the eclosion of the first workers and why fighting and killing of all but one of the queens occur soon after the worker eclosion. What remains to be demonstrated is that the probability of becoming the surviving queen is modulated according to the values of  $x$  and  $k$  in the ways predicted by the concession or restraint model or is unaffected by these variables as predicted by the pure tug-of-war model.

## Reproduction in Mother-Daughter vs Same-Generation Groups

As shown by Reeve & Keller (77), there is considerable evidence that skews are higher when dominants are mothers of subordinate females than when dominants are of the same generation as subordinate females, as predicted by transactional theory but also by tug-of-war theory (75). An associated prediction is that aggression should be higher in sister groups than in (singly mated) mother-daughter groups

because the effective window of selfishness is zero in the latter (73). Recent studies of a ponerine ant (*Diacamma* sp.) show that the queen or gamergate is morphologically just a worker (a queenless caste is absent), but the skew is high regardless of whether subordinates are full sisters or daughters (50, 104). However, complete skewing in sister associations is accomplished by aggression, whereas complete skewing in mother-daughter associations appears to be accomplished peacefully (possibly via contact pheromones) in accordance with the window-of-selfishness model.

The Reeve & Keller (77) model assumes that subordinates respond only to their mean relatedness to the dominant's offspring. If subordinate workers and dominant mothers can assess their relatedness to male- and female-destined eggs separately, workers may gain by selfishly attempting to replace the queen's sons with their own sons, even if ecological constraints are sufficiently harsh to create complete skew—that is, the window of selfishness can be wide for male production even though it is effectively of zero width for female production (73). This hypothesis accounts for the behavioral conflicts (and high skews) between queens and daughter workers in relatively small hymenopteran colonies like polistine wasps and bumblebees (reviewed in 23, 55, 71) and in ponerine and leptothoracine ants (6).

## Differential Oophagy: A Puzzling Phenomenon Illuminated by Transactional Models

In many if not most of the insect societies with low reproductive skew, dominants and sometimes subordinates frequently eat and replace each other's eggs (which is called differential oophagy) but typically ignore each other while these eggs are being laid (37, 71). Why don't group members in these low-skew societies directly challenge oviposition attempts by others? The transactional models provide an elegant explanation for this phenomenon. In low-skew societies, the reproductive payments required by group members for group cooperation should be relatively large (according to concession theory), and, if direct interference of oviposition occurs, the benefits of grouping are at high risk of being lost through group dissolution (dispersal or lethal fighting). Thus, the prudent selfish strategy is to allow oviposition by another group member (increasing the latter's assessed reproductive share) and then to later remove and replace the latter's egg (under the guise of egg inspection or while the opponent is occupied elsewhere). Mutual oophagy is likely to be evolutionarily stable even if it has no net effect on the skew, because a restrained, nonselfish mutant would suffer reduced reproduction.

Of course, there are other hypotheses for why differential oophagy rather than direct challenge occurs. For example, differential oophagy yields a nutritive benefit without the risk of physical confrontation. However, this hypothesis by itself does not explain why differential oophagy seems associated with low reproductive skew. The transactional hypothesis could be tested further by observing whether differential oophagy changes to direct confrontation as skew increases in the same colonies.

## TESTS OF REPRODUCTIVE-SKEW THEORY IN LARGE INSECT SOCIETIES

### Leptothoracine Ants

In a pioneering study, Bourke & Heinze (8) investigated the factors underlying variation in reproduction among nestmate queens in the genus *Leptothorax*, a group of ants particularly suitable for such studies because of their extreme diversity in social organization and their small colony sizes (relative to those of other ants). These authors found that the degree of reproductive skew increases with greater ecological constraints on dispersal, the latter inferred from the amount of patchiness in suitable nesting habitat (8, 32, 33). This finding supports the transactional-concession model.

A positive association between queen-queen relatedness and reproductive skew also was found. In some *Leptothorax* species, all queens contribute to reproduction (polygyny), whereas in some others, a single queen monopolizes all of the reproduction (functional monogyny). As predicted by concession models, the relatedness among nestmate queens is higher in the functionally monogynous species (high skew) than in the polygynous species (lower skew) (8, 32). The association of high skew with high relatedness is also exhibited between different populations of the ant *Leptothorax acervorum* (7) as well as among species of different genera (75).

Bourke & Heinze (8) also found that higher reproductive skew was associated with higher levels of within-group aggression, as predicted by the window-of-selfishness transactional model of within-group conflict. The coupling of low skew with low levels of within-group aggression is found not only in leptothoracines but also in ponerines, another ant taxon with typically small group size (62, 102).

Although these data together indicate that high skew is associated with high relatedness in ants, caution is necessary because data are yet available for only a few species (or few colonies per species) and the frequency of parent-offspring associations, particularly in the functionally monogynous species, has yet to be investigated (which is important because both transactional and tug-of-war models predict high skews in parent-offspring associations). Moreover, as Heinze (32) pointed out, high relatedness among queens within colonies might result from high skew (rather than the reverse) when queens are readopted into their native colony, as indeed is probably the case in many polygynous ant species (12, 45, 96, 98). Finally, queen number and other social attributes may be a confounding variable in these analyses.

An even more crucial issue is the extent to which workers affect the reproductive partitioning and stability of groups the size of leptothoracine colonies and larger. For example, many highly polygynous ants reproduce via budding, a process in which queens and their workers depart from their mother colonies to initiate new colonies. Clearly, the workers' genetic interests must strongly influence such aspects of colony reproduction. We next consider how worker interests should



influence reproductive partitioning, group size, and conflict within large insect societies.

## The Workers as a Collective Dominant

In very large colonies of ants, bees, and wasps, workers play a key role in determining both the number of queens and the latter's relative contribution to reproduction (49). Moreover, queens get almost all of their food from workers. Because of their sheer numerical superiority, the worker collective could itself be viewed as a dominant in such societies, with the reproductive shares within the colony being distributed according to the workers' aggregate genetic interests.

Interestingly, the structure of transactional theories of skew is unaltered under this "workers-as-the-dominant" picture (HK Reeve & RL Jeanne, submitted for publication). For example, consider a large colony in which there are two queens symmetrically related by  $r$  and a large number of workers acting as a collective dominant. Assuming for the moment that the workers themselves are nonreproducing and that they are related on average by  $r_1$  to the first queen's offspring and  $r_2$  to the second queen's offspring ( $r_1 < r_2$ ), the workers should act so as to maximize their mean inclusive fitness.

$$r_1pk + r_2(1 - p)k, \quad (4)$$

where  $p$  is the fraction of reproduction obtained by the first queen (also see variables in Table 1). It is easy to see that the workers will do best if they treat the second queen as the dominant queen (who becomes a "virtual dominant") and give the first queen only its minimal staying or peace incentive (to keep it from leaving or fighting the other queen) if retaining that queen is beneficial. Note that only the concession model should apply in this case because the numerically predominant workers should control not only the queens' reproductive shares but also group membership. The key result is that the magnitude of the first queen's staying incentive and the conditions under which this incentive is given and the first queen retained or ejected are exactly the same as for the basic concession model in which the second queen is behaviorally dominant to the first queen (Table 2). In other words, the first queen's staying incentive is still that described by Equation 3, where  $r$  is the relatedness between queens (this is the relevant  $r$  because the two queens are still the only reproducing colony members).

One can also allow for the possibility that one or more of the workers are allowed to reproduce by the worker aggregate. For example, suppose there is a single queen to whose offspring the worker aggregate is (on average) related by  $r_q$  and also a potentially reproductive worker to whose offspring the worker aggregate is related by  $r_w$ . The worker aggregate will then maximize

$$r_qpk + r_w(1 - p)k. \quad (5)$$

The workers will treat the queen as the dominant if  $r_q > r_w$  and the worker as the dominant otherwise. Again, solutions to the basic concession model apply, with

the important implication that transactional-skew theory can quantitatively predict the extent of worker reproduction in the colony, as well as the conditions under which workers will evict the breeding worker or the queen. {The latter condition is  $[r_q pk + r_w(1 - p)k] < (r_q x + r_w)$ , where  $p$  is the staying incentive from Table 2. This reduces to  $[(r_w - rr_q)(k - 1 - x)(1 - r)] < 0$  or just  $x > (k - 1)$  because  $(r_w - rr_q) > 0$ .} In summary, the only addition to the basic concession model is the rule that the virtual dominant will be the individual to which the workers have the greatest average relatedness.

An important assumption of the worker-as-collective-dominant hypothesis is that workers can somehow determine their expected relatedness to nestmate queens. Previous studies of large colonies of ants, wasps, and bees have generally demonstrated that workers do not favor more closely related individuals within colonies, for example by using genetically variable cues (reviewed in 46). Hence, workers may have to use indirect cues to assess differences in their statistically expected relatedness to queens. For example, when a monogynous colony recruits a new queen, the latter queen can either be a sister of the workers (if recruitment occurs from within the nest) or an unrelated queen. If the recruited queen is unrelated to the workers, the workers should treat the mother resident queen as a virtual dominant. If the recruited queen is a sister, workers should favor their mother for female production or both male and female production if workers cannot readily identify the sex of the brood early in the development (see below). Discrimination between the resident mother queen and the newly accepted queen is possible on the basis of between-colony odor differences (if the queen comes from another colony) or differences in age or prior social experiences (if the recruited queen is a sister).

Workers also can indirectly assess their expected relatedness to queens based on the fecundity differences among those queens. The most fecund queens will have the highest mean relatedness to workers because they will have produced the largest fraction of workers. Indeed, workers are able to assess queens' fecundities in colonies of eusocial insects (22, 48, 63). Moreover, differences in queens' fecundities are used as proximate cues by workers to determine which queens are accepted within colonies. In the monogynous form of the fire ant *Solenopsis invicta*, for example, queenless workers will generally retain the most fecund queen and kill the other when given the choice of two queens differing in fecundity (22, 48, 91).

We next examine whether the "workers-as-the-dominant" concession model successfully accounts for variation in reproductive partitioning and queen number in large-colony eusocial insects. To the extent that this model fails, other (mostly undeveloped) models will have to be invoked, such as a many-person tug-of-war model (75).

## Partitioning of Reproduction Among Queens

We know of no well-documented case of workers providing staying incentives to subordinate queens in large colonies of eusocial Hymenoptera. In all species in

which a queen monopolizes reproduction (e.g. functionally monogynous ants and ponerine colonies), the dominance hierarchy and partitioning of reproduction arise after fights between queens. Fights are typically intense until one queen becomes dominant. Once dominance has been established, workers frequently play an important role in maintaining the hierarchy and preventing the subordinates from reproducing. For example, queens of *Leptothorax* sp. A engage in vicious fights just after hibernation, until one queen becomes dominant and monopolizes all or most of the colony reproduction (33). Once the dominance is established, queens stop fighting, and workers attack and expel subordinates that initiate ovary development later in the season. Thus, here is clearly a case in which workers enforce complete skew.

What is lacking is a case demonstrating that workers actively direct reproductively valuable resources to a subordinate queen as part of a positive staying or peace incentive (as opposed to determination of these resource flows strictly by queen-queen interactions). It remains to be investigated why this is so. One possibility is that stable associations of queens in the presence of workers and partial skew in the production of reproductive members together occur so rarely that such systems simply have not been studied. However, it may also be that workers allow concessions of staying incentives to proceed strictly via queen-queen interactions, because, as shown above, the workers and the queen to which they are most closely related have identical views of how reproduction should be partitioned among the queens (when the workers themselves do not reproduce). Moreover, it may be that the workers (unlike queens) do not have sufficiently reliable cues for assessing the relatedness  $r$  between queens that enters into computation of the subordinate queen's staying incentive (Table 2). The evidence required for documenting worker-mediated as opposed to queen-mediated staying incentives in low-skew societies would have to show that, when the virtual dominant from the worker's point of view is not the same as the behaviorally dominant queen (in the absence of worker influence), the reproductive skew is that reflecting worker interests, with the behaviorally dominant queen becoming the "virtual subordinate" and receiving only a staying incentive.

Three recent studies have investigated whether reproductive skew correlates with intrapopulational variation in queen-queen relatedness in species with large colonies, and the available data do not support predictions of the original concessions model. In the polygynous ant *Myrmica tahoensis*, Evans (20) found that skews were near zero independently of interqueen relatedness, which was high on average ( $r = 0.58$ ) but quite variable (29% of queen pairs were distant relatives). Aggression between queens was very low, again regardless of relatedness. Similarly, in *Leptothorax ruatus*, skew (measured as egg-laying rate) was low and there was no significant association between skew and queen-queen relatedness (average  $r$ : 0.40, range 0.0–0.7, Rüpell, unpublished). The skew in the production in male and female sexuals was significantly negatively correlated ( $r = 0.69$ ) with queen-queen relatedness, in clear contrast with the prediction of concession models. Similarly, M Hannonen & L Sundström (unpublished) found

that skew decreased with increased queen-queen relatedness in the ant *Formica fusca*. Relatedness between queens was again relatively high in the later species and skew between queens relatively small. Overall, these data sharply contrast with predictions of the original concession models, although variation in other factors possibly affecting skew ( $k$ ,  $x$ , and group size) apparently was not taken into account.

Assuming that the above studies do not suffer from confounding variables, they imply either that intrapopulational variation in relatedness cannot be assessed by workers or queens; or a model different from the original concessions model, such as the tug-of-war model, applies. One particularly interesting possibility is that the bidding game model applies. Workers, in effect, bid for the services of queens which can move between colonies [a possibility raised by Evans' study (20)]; the model predicts that skew and aggression should be generally low and independent of queen-queen relatedness [which is predicted to become quite variable (72)]. The bidding game requires that there be colony-level benefits to adding subordinates; therefore, it is important to determine whether recruiting new queens in fact increases colony success.

## Worker Production of Males

The workers-as-the-dominant concession model yields the simple prediction that workers should not produce reproductive females in the presence of the mother queen, who should always be the virtual dominant with respect to reproductive female production. This is true because, whatever the mean relatedness  $r$  between the workers and the queen's female offspring, the mean relatedness between the workers and another worker's female offspring will have the lesser value  $r/2$ . [Note from the earlier discussion that this line of reasoning does not necessarily apply for small insect societies in which a dominant queen must take into account an individual subordinate's relatedness to its own offspring (one-half) versus the subordinate's relatedness to the queen's offspring ( $r$ ). For example, one-half relatedness can exceed  $r$  if the queen is multiply mated.] Indeed, the data for large eusocial hymenopteran colonies overwhelmingly supports this prediction, in large part because workers have lost the ability to mate and thus produce female offspring (6, 55, 110). Of course, the latter fact by itself is explained by this prediction of the workers-as-the-dominant concession model.

The model makes the straightforward prediction that the queen in large societies will be allowed by workers to produce males as a virtual dominant if workers are on average more closely related to the queen's male offspring than they are to the male offspring of other workers. Thus, in a single-queen society, the workers should produce all of the male offspring if the queen has effectively mated with fewer than two males, and the queen should produce the male offspring if she has effectively mated with more than two males. This is known as worker-policing theory (69), which now emerges as an important special case of the workers-as-the-dominant concession model (HK Reeve & RL Jeanne, submitted for publication).

The theory has received experimental support in honey bees (70) and also nicely accounts for the finding that worker production of males is rare in honey bees (*Apis*) but quite common in stingless bees (*Melipona* spp.), in which the queen is singly mated (64). Worker-policing theory also predicts that male production by workers, even if socially inhibited in the presence of a multiply mated queen, should occur commonly if the queen should die. There is abundant support for this prediction in honeybees, bumblebees, and ants (reviews in 6, 55, 77, 110).

In societies with an effective number  $n$  of singly mated queens having relatedness  $r$ , policing theory predicts that male production by workers will occur if  $n < (1 + 1/r)$  (6, 59). Obviously, if the queens are unrelated, the prediction is that workers should always produce the males. There are surprisingly few data to test this hypothesis, although worker production of males in the ant *Myrmica rubra* is known to occur along with a frequently low relatedness among probably singly mated nestmate queens (review in 6, 61). Conversely, in colonies of neotropical swarm-founding wasps, in which there are typically multiple queens of high relatedness, male production is largely restricted to queens, and workers are more closely related to other queens than to each other, again in support of the model (31).

Despite this early empirical support, there are numerous exceptions to the predictions of the worker-policing theory and thus the workers-as-the-dominant concession model. Bourke (5) found that worker production of males in queen-right ant colonies occurs mostly in polygynous species (in which relatedness among queens may typically be low) and infrequently in monogynous species. In particular, there are numerous ant societies in which there is only a single, singly mated queen, yet the workers produce none of the male offspring, in apparent contradiction to policing theory (6, 34). Explanations of such cases may have to take into account other factors, such as potential losses in colony efficiency if workers were to assume male production as well as performance of colony tasks (6).

However, it is also possible that ant queens actively enhance uncertainty over the sex of their eggs to achieve complete skew even in male production. If the workers' assessed relatedness to each of the queen's young brood is uniformly one-half instead of three-fourths for sisters and one-fourth for brothers, owing to lack of discriminability of brood sex (6, 56), then parent-offspring transactional models predict complete skew in production of both males and females (77). By the time that workers can discriminate the sex of a maturing brood, it may not be beneficial for workers to substitute worker-laid male eggs for maturing brothers because the latter will have a higher reproductive value (56). The cost of this sexual deception may be that workers will not be able to optimize the care of a brood of unknown sex, if the sexes have different nutritional optima (indeed, such a cost may be especially high in the mass-provisioning meliponines, possibly accounting for why queens in those species do not benefit from hiding the sex of eggs). This hypothesis may explain why Bourke (5) found queen-right worker reproduction primarily in polygynous ant colonies—in the latter, enhancement of uncertainty of brood sex by queens is less beneficial relative to its costs because reproduction

by multiple queens by itself will tend to reduce the asymmetry in mean worker relatedness to male vs female broods.

## Worker Control of Queen Number and Identity

The  $N$ -person concession model, now with workers viewed as a collective dominant, makes the prediction that there will be a negative correlation between queen-queen relatedness and queen number (the same correlation also is predicted for small-colony species). The reason is that the indirect kin-selective benefit a dominant receives from a solitarily nesting subordinate goes up as the relatedness between subordinate and dominant increases (74). Intriguingly, this is exactly what is found for multiqueen ant societies (45). Moreover, queen numbers increase as the ecological constraints on solitary founding increase, also in accordance with the  $N$ -person model (45).

The workers-as-the-dominant concession model also makes quantitative predictions about the conditions under which workers should evict or kill other queens, as well as which queens should be so treated. A subordinate queen (the queen having the lesser mean relatedness to the workers) should be evicted and forced to breed elsewhere if  $x > (k - 1)$ , that is, when the queen's contribution  $k$  is sufficiently low and constraints on solitary breeding are sufficiently weak ( $x$  high).

In the Reeve & Ratnieks (82) concession model that includes fighting options, there is another possibility for a reduction in queen number. If the subordinate queen would actually reduce colony productivity ( $k < 1$ ), for example because she is an energy drain and her presence does not benefit the colony, then this queen would tend to be killed rather than leave the colony provided that  $f > x/(1 - r)$ . Here  $f$  is the probability that the queen will escape worker execution, a probability that could be quite small but should be above zero because there is a chance that the workers will have mistakenly assessed the other queen as the subordinate. (By the time the subordinate queen is attacked, immediate injury would likely make the expected solitary success fall rapidly to zero if it is not already zero, so that even an injured queen does better by remaining in the colony until the bitter end.) Thus, workers should be observed to execute the subordinate queen when ecological constraints are strong and the relatedness between queens is sufficiently low. A lethal fight occurs under these conditions because the subordinate does better to risk execution by workers than to leave for an extremely low payoff for solitary breeding.

The latter model is in accord with data on queen executions in foundress (pleometrotic) associations of ants. In most such associations, relatedness between queens is zero, and workers execute (or participate in executing) all but one of the queens shortly after worker emergence (4, 35). Such associations typically form under extreme ecological constraints on solitary breeding, as evidenced by the high frequency of pleometrotic nest foundation. Once the workers emerge, the contributions of the auxiliary queen(s) fall dramatically (because workers take over the colony tasks), and the presence of these auxiliary queens likely yields a net cost to the colony ( $k < 1$ ). Because ecological constraints are high, that is,

$x$  appears to approach 0 especially by worker emergence and relatedness is zero, the queen execution condition is highly likely to be met [ $f > x/(1 - r)$  becomes approximately just  $f > 0$ ]. That is, lethal fighting (i.e. queen executions) will occur even if the subordinate queen has only a small probability of surviving or somehow avoiding execution.

In fire ants, workers appear to participate in queen execution only after the queen hierarchy has become clear and especially after one of the queens has been damaged in fights with the other queen(s) (1). However, this is not inconsistent with the concession queen-execution model because workers cannot identify their mother queen directly (1), perhaps because maternal recognition cues have been suppressed or scrambled (72). The workers' best option apparently is to let the queens fight among themselves first, because the queen most likely to win the fight [typically the largest-headed queen (2)] is also the queen that produced the most workers (3). Thus, initially allowing the queens to fight actually provides a mechanism for workers to establish which queen is on average most closely related to them. The workers then benefit by joining in attacks on the losing queen, in accordance with the execution model.

The concession-based queen execution model also neatly explains the regulation of queen number in swarm-founding neotropical wasps. Swarms usually contain multiple queens together with workers (39). At variable times after swarms establish new nests (and new workers emerge), workers appear to maul and kill multiple queens, reducing the queen number to very few or even one (28, 39, 109), creating the pattern called "cyclical oligogyny." Presumably workers are eliminating queens to whom they have lower expected relatedness (e.g. as inferred through differential fecundity if the workers are descended from the queens), although this needs to be verified. Thus, the condition for queen killing [ $f > x/(1 - r)$ ] is plausibly satisfied given that ecological constraints on independent breeding are known to be high ( $x$  low) for neotropical wasps because of extremely high levels of ant predation [to which swarming is presumably an adaptation (39)].

Later in the colony cycle, when the queen number has been reduced to one and the colony is now bigger, new queens are produced that are not killed by workers but instead leave the natal colony in new swarms. This pattern also makes sense in light of the concession-based queen execution model; when the colony is larger, the founding success of new swarms is higher because each swarm can be bigger, likely causing  $x$  to increase and thus  $f$  to no longer be larger than  $x/(1 - r)$ . Moreover, the mean relatedness of workers to the new queens may exceed the mean relatedness of workers to the old swarm queens at the time of queen execution. Such a relatedness increase makes  $f > x/(1 - r)$  even less likely late in the colony cycle, reinforcing the effect of increasing  $x$ . Thus, instead of being executed, it makes sense that the late-season queens readily found new colonies with attendant workers in swarms according to the leaving condition  $x > (k - 1)$ .

Finally, the concession-based queen eviction model may explain differences in the patterns of queen eviction between colonies of stingless bees, which have a single, singly mated queen, and honey bees, which have a single, multiply mated

queen (64). In stingless bees, the mother queen remains behind at the parental colony as one of her daughter queens takes off in the new swarm. However, in honey bees the pattern is reversed. The question naturally arises in the context of the concession-based queen eviction model: Is the mother queen the virtual dominant among stingless bees, explaining why the daughter queen is the one who leaves (as a subordinate), and is this reversed in honey bees?

In the workers-as-the-dominant view, the virtual dominant is the queen to whose offspring workers have the greatest genetic value. If the mother queen effectively mates with  $m$  different males, the kin value of the mother queen's offspring to workers, if we assume worker sex ratio control, an equilibrational sex ratio, and take into account the reproductive value of males, is  $(2 + m)/4m$ . [The kin value equals the ratios of investment in males times the relatedness to males times the mean number of females per male plus ratio of investment in females times the relatedness to females (59).] If the workers are on average related by  $r$  to the daughter queen, the mean kin value of the daughter queen's offspring is equal to  $r(2 + m)/2(1 + m)$  (assuming that most workers in the population are working for their mother, which the daughter queen will become once she begins producing her own worker offspring).

Thus, in stingless bee colonies with singly mated queens,  $m = 1$  and  $r =$  three-fourths, meaning that at the time of swarming the queen's offspring are worth 0.75 to the workers and the daughter queen's offspring are worth 0.56 to the workers. This yields the correct prediction that in stingless bees the mother will be the virtual dominant, and it will be the daughter queen who leaves with the swarm like a subordinate under the condition  $x > (k - 1)$ .

In contrast, in honey bee colonies with 12 effective matings by the mother queen, the mother queen's future offspring are worth only 0.30 to the workers on average. For the daughter queen's offspring to be worth  $>0.30$  (making the daughter queen the virtual dominant), the mean relatedness  $r$  of the daughter queen to the workers controlling the identity of the staying queen must be at least 0.54. (The latter threshold relatedness declines as the effective mating frequency  $m$  increases.) In other words, the workers in control of virtual dominance (e.g. the currently dominant patriline of workers in the colony) must have some mechanism of favoring a daughter queen who is their full sister with a probability of  $>0.58$ , if the concession-based eviction model is to make the correct prediction about which queen leaves with the swarm. The latter calculation shows that such recognition may be quite sloppy and still lead to elevation of a daughter queen to the status of a virtual dominant, forcing the mother queen to leave with the swarm as a subordinate. Genetic studies will settle whether the myriad aggressive and protective interactions between workers and new queens just prior to swarming manifest the required level of patriline favoritism. Such nepotism does not appear to occur in the contexts of queen rearing or swarm membership, but recent evidence suggests that worker nepotism might still influence the outcome of fights among preswarming queens (100).



## CONCLUSIONS

Despite the fact that tests of skew theories in social insects are still at an embryonic stage, our review reveals that some of these theories are already receiving taxonomically widespread support. Recent authors have suggested that evidence supporting transactional models of skew is sparse or merely indirect (14, 21), but our survey indicates that both conclusions are too pessimistic. In small-colony social insects in which complete reproductive control by a single individual is plausible, the transactional-concession models overall account better than does any other existing model for the observed relationships between each of the dependent variables of skew, changes in reproductive partitioning over time, group size, and within-group aggression, and each of the predictor variables of genetic relatedness, ecological constraints on solitary breeding, and benefits of group living.

Our review supplements the conclusions of a concurrent review on the concession model prediction of a positive relationship between skew and relatedness. Sumner & Isaacs (99) conducted a phylogenetic analysis of the association between queen-queen genetic relatedness and reproductive skew using data for 13 Vespidae, one Sphecidae, one Apidae, and six Formicidae species. Their analysis showed a strong positive association between the two variables even when phylogenetic nonindependence is statistically controlled, with 13 of the 17 independent contrasts showing an increase in skew associated with an increase in relatedness. Although these data provide support for transactional models, some caution is necessary because some species comprised groups of mother-daughter associations [which tug-of-war theory also predicts will have high skew (75)], and skew estimates were likely inflated owing to heightened sampling error in species in which maternity could be assigned for only a few offspring.

This early success of concession as opposed to restraint models raises the question of which assumptions of the latter are typically violated. One possibility is that the assumption that one individual (the dominant, by definition) controls group membership and the other individual (the subordinate) controls reproductive shares may not often be satisfied. For example, the characteristics that empower an individual to control group membership (e.g. size or age) may also typically be the same characteristics that empower an individual to control reproductive shares within the group. In the latter case, the concession model must be more applicable.

The extension of transactional concession models via the workers-as-a collective-dominant model potentially offers new insights into some of the most striking reproductive patterns in large-colony eusocial Hymenoptera, from the loss of worker ability to produce female offspring to patterns of skew and aggression in polygynous societies. By linking skew theory to worker-policing theory, this general model suggests new and testable explanations for the apparent exceptions to policing theory. The expanded concession model also provides a unified explanation for diverse patterns of worker control of queen number and generates many new testable predictions.

Testing the assumptions of skew theory, such as the complete-control assumption for small groups, is an important new direction for skew research. For example, in cases of shared reproduction, concession models predict that experimental reduction of the subordinate's reproductive share (in a way that allows the subordinate to assess the reduced share) should trigger leaving or fighting by the subordinate, and restraint models predict that experimental reductions in the dominant's reproductive share will trigger eviction of the subordinate by the dominant.

Future tests of skew theories also must continue to test the families of predictions associated with each of the alternative skew models and not just focus on one predictor variable such as genetic relatedness. The skew models are now of sufficient complexity to generate predictions not only about reproductive skew but also about group size and within-group aggression, which together expand each family of predictions. Such expansion should lessen the handling times associated with tests of the skew models and speed progress toward uncovering the general principles of social evolution.

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