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Reproductive Skew and the Origin of Sterile Castes

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ABSTRACT: Reproductive skew theory has not heretofore formally addressed one of the most important questions in evolutionary biology: How can whole-life sterile castes evolve? We construct a transactional skew model investigating under what conditions a subordinate in a multimember group is favored to develop into a morphologically specialized worker caste. Our model demonstrates that, contrary to former expectations, the ecological and genetic conditions favoring caste differentiation are far more restrictive than those favoring high skew. Caste differentiation cannot be selected in saturated, symmetrical relatedness groups unless the genetic relatedness among group members is extremely high. In contrast, it can be selected in the saturated, asymmetrical relatedness (parent-offspring) groups with complete skew. If we also consider the future reproduction of subordinates, caste differentiation is possible only after the group size reaches a certain critical point. Most importantly, caste differentiation in a parent-offspring group increases its saturated group size. The positive feedback between group size and the degree of caste differentiation can continue in principle until completely sterile worker castes emerge. Thus, at least in the case of parent-offspring groups, group size but not the degree of reproductive skew may be a better index of the level of social complexity. A scheme for the evolution of sterile worker castes that integrates the role of group size into the framework of reproductive skew theory is proposed.

Keywords: caste differentiation, eusociality, group size, reproductive potential, reproductive skew, totipotency.

Reproductive skew theory aims to explain the extent to which reproduction is biased within animal societies. In high-skew societies, one or a few individuals monopolize reproduction; in low-skew societies, reproduction is dis-

tributed more equitably. It integrates genetic relatedness effects, ecological constraints on solitary breeding, and group-living benefits into a single framework, which researchers have claimed provides a unified theory for social evolution (reviews in Keller and Reeve 1994; Bourke 1997; Emlen 1997; Reeve et al. 1998; Johnstone 2000; Reeve and Keller 2001). With the rapid development of reproductive skew theory over the past few years, a number of different models and their unique predictions have been suggested. Two basic categories of skew models—classical optimal skew models, or “transactional” models (Vehrencamp 1979, 1983*a*, 1983*b*; Emlen 1982*a*, 1982*b*; Reeve 1991, 1998, 2000; Reeve and Ratnieks 1993; Johnstone et al. 1999; Reeve and Emlen 2000), and incomplete control models, or “tug-of-war” or “compromise” models (Cant 1998; Clutton-Brock 1998; Reeve et al. 1998; Johnstone and Cant 1999)—have been identified. In addition, many other possible factors, such as asymmetry in fighting abilities, relatedness asymmetry in parent-offspring associations, multimember group size, and resource inheritance by subordinates, have been proposed to influence the degree of skew (see Johnstone 2000; Reeve and Keller 2001).

All previous skew models have assumed that every individual in a group is totipotent, that is, able to engage in both reproductive and helper roles equally successfully (Crespi and Yanega 1995; Crespi and Choe 1997*b*; Bourke 1999). Most attempts to test predictions of various skew models have thus been confined to species without morphological castes, such as “primitively” eusocial insects (e.g., Reeve and Nonacs 1992; Field et al. 1998; Reeve et al. 2000) and cooperatively breeding birds and mammals (e.g., Clarke and Faulkes 1997, 1998; Jamieson 1997; Heinsohn et al. 2000; Clutton-Brock et al. 2001; De Luca and Ginsberg 2001), or to some “advanced” eusocial species that harbor multiple-queen colonies (e.g., Bourke and Heinze 1994; Heinze 1995; Bourke et al. 1997; Fournier and Keller 2001).

As a result, the so-called unified evolutionary social theory has not yet been applied to the question of the origin of nontotipotency, that is, the origin of morphologically specialized worker castes. This question, which traces back to Darwin (1964), has been at the core of social evolution studies since Hamilton (1964), and it has generated a large

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body of theories and tests (e.g., Wilson 1971, 1975; Hamilton 1972; Alexander 1974; West-Eberhard 1975; Evans 1977; Vehrencamp 1979; Andersson 1984; Alexander et al. 1991; Seger 1991; Bourke and Franks 1995; Bourke 1997; Choe and Crespi 1997; Queller and Strassmann 1998). Historically, three hypotheses have been proposed to explain the evolution of sterile worker castes, although they are not mutually exclusive: high relatedness and haplodiploidy (Hamilton 1964, 1972), mutualism (Lin and Michener 1972), and parental manipulation (Alexander 1974). The causal factors considered by these hypotheses are fundamentally the same as those used in skew models: relatedness to one's own offspring versus helped individuals, ecological constraints on independent reproduction and colony-productivity benefits from helping (see also Brown 1987), and power asymmetries between incipient reproductives and workers. Currently, morphological castes are presumed to evolve when within-group relatedness is reasonably high (at least 0.25 and often 0.50 or greater) and under specific ecological conditions involving one of the following: either short life span of adults relative to juvenile development time, which selects for helping via the inclusive fitness benefits by helping soon after reaching adulthood (Queller 1989; Gadagkar 1990), and having the "life insurance" for brood provided by surviving colony-mates (Queller and Strassmann 1998); or habitats that combine food and shelter (e.g., wood, galls, or burrow systems), which are extremely valuable "super-nurseries" and provide a context where defense, excavation, and nursing provide exceptionally strong kin-selected benefits (Alexander et al. 1991; Crespi 1994; Queller and Strassmann 1998). Despite the success of these ideas in helping to explain the taxonomic distribution of species with worker castes, they have yet to be formalized into mathematical models that explicitly predict the conditions under which social totipotency is lost.

In fact, a few skew researchers have already argued, though briefly and verbally, that reproductive skew in species with morphological castes is settled mainly by caste membership (Keller and Reeve 1994, 1998). They suggested that the ultimate factors that induce subordinates to become morphologically specialized workers would be basically the same as those favoring high skew. They also stated that individuals should develop into worker castes over evolutionary time only when there is a low prospect of successful breeding through one's life, the relatedness among group members is high, worker castes significantly increase group productivity, and worker castes are likely to remain all their life with kin that can benefit from their help (Keller and Reeve 1998). What is needed now is to construct a corresponding skew model and derive testable predictions from it. Moreover, to do so would give new insight into the recent debate over social terminology

(Gadagkar 1994; Crespi and Yanega 1995; Sherman et al. 1995; Costa and Fitzgerald 1996; Crespi and Choe 1997a, 1997b; Nonacs 2001). The main point at issue was whether the irreversibility of castes represents an evolutionary threshold that indicates differences between societies both in the nature of their behavioral interactions and in the selective pressures that have shaped them. Developing a skew model for how sterile castes have originated, hence, would also benefit the resolution of the controversy.

Building on the transactional framework of skew models (Reeve 1991; Reeve and Emlen 2000), we present a skew model investigating under what conditions a subordinate in a multimember group is favored to develop into a specialized morphological worker caste rather than retain its totipotency. We assume that a newly evolved worker caste that is no longer totipotent should increase group productivity as compared with when everyone is totipotent (Bourke 1999), since a worker caste that partially or entirely foregoes reproduction may be more able to perform tasks beneficial to the group. We show that, contrary to former expectations, conditions favoring the evolution of morphological castes are clearly distinct from those favoring high skew. We also demonstrate that, in explaining the evolution of phenotypic divergence into breeder and worker castes, not the degree of reproductive skew but the group size reflects the level of social complexity more successfully. Finally, we propose a scheme for the evolution of sterile worker castes within the framework of reproductive skew theory.

The Dyadic Transactional Model of Caste Differentiation

Symmetrical Relatedness, Positive Staying Incentives (Partial Skew)

We begin with the transactional model of skew for dyadic groups that are composed of a dominant and a subordinate. We first treat the case of symmetrical relatedness groups where the dominants and subordinates are symmetrically related to each other's offspring. For simplicity, we will not be concerned with the "peace incentive" of Reeve and Ratnieks (1993). Classical "concession" models, one of the two main transactional models of skew, assume that the dominant fully controls subordinate reproduction and that the subordinate has two options, that is, staying in the group and helping or leaving the group and reproducing independently (Vehrencamp 1983a, 1983b). Under these assumptions, concession models seek the conditions under which the dominant should yield just enough reproduction to the subordinate to make it favorable for the subordinate to stay in the group rather than disperse.

Transactional skew models consider several parameters:

x is the expected solitary reproductive output by a subordinate relative to the expected reproduction of 1.0 for a lone breeder (assumed to be $0 < x < 1$); k is the total productivity of the dyad (assumed to be $k > 1$, and its magnitude is independent of who is the parent of the offspring); r is the genetic relatedness between the two parties. Hamilton's rule (Hamilton 1964) states that, for two alternative strategies, a strategy i is favored over the other strategy j if

$$P_i + rK_i > P_j + rK_j, \quad (1)$$

where P_i (or P_j) is the direct reproduction associated with strategy i (or j) and K_i (or K_j) is the other party's direct reproduction when strategy i (or j) is performed.

If ecological constraints are sufficiently strong, the subordinate will remain in the group even with no reproduction; inequality (1) specifies this condition as $x < r(k - 1)$. If ecological constraints are moderate, the subordinate will require the dominant to donate a fraction p of total group productivity (termed "staying incentive") in return for its staying in the group and helping. The staying incentive is given as follows (Reeve and Ratnieks 1993):

$$p = \frac{x - r(k - 1)}{k(1 - r)}. \quad (2)$$

It is necessary to ask whether the dominant will be favored to offer the staying incentive rather than eject the subordinate. Applying inequality (1) from the viewpoint of the dominant, we find it is possible when $x < k - 1$. The staying incentive, therefore, should be offered only under the condition $r(k - 1) < x < k - 1$. If ecological constraints are weak, the dominant will not concede the staying incentive and the subordinate will not join; this condition is given by $x > k - 1$ (Reeve and Ratnieks 1993).

Here we add another assumption that a totipotent subordinate in a stable group can choose to develop into a morphological worker caste, leaving untouched the basic formats of the transactional skew framework that the dominant concedes a minimum share of reproduction to a subordinate in return for the latter's staying in the group and that, if the subordinate were to receive less than its minimum share, it would choose to disperse. By developing into an irreversible worker caste, the subordinate will be able to enhance significantly the group productivity with its specialized morphology, though it must suffer the loss of its totipotency (Crespi and Yanega 1995; Crespi and Choe 1997*a*, 1997*b*). To take this possibility into account, we define w as the reproductive potential of a worker caste (relative to a standardized reproductive potential of 1.0 for the dominant or the subordinate before "deciding" to

become a worker), which represents the extent to which workers are nontotipotent relative to a "totipotent" individual (assumed to be $0 \leq w < 1$; Bourke 1999). Note that totipotency has been formally defined as the potential to express the full behavioral repertoire of the population and the ability to produce offspring without help (Crespi and Yanega 1995). In some primitively eusocial bees, for example, differences in larval nutrition causes gynes and workers to differ in size but not in form (Wheeler 1986). The workers' smaller body size circumscribes their reproduction should they gain the opportunity to reproduce. By comparison, most ant workers are unable to mate and produce female offspring because they lack a spermatheca, and they usually produce male offspring only in queenless colonies (Bourke 1988; Choe 1988). Hence, it can be said that the former workers have higher reproductive potential compared with that of the latter workers. In a few ant species where the functioning ovaries of workers are absent, the workers are totally sterile and w may equal 0 (note that we are also concerned about quantitative differences among the extent of nontotipotency, whereas Crespi and Yanega's [1995] original concept of "totipotency" consists only of its presence or absence).

We assume that whenever the newly evolved worker caste attempts to reproduce, its reproduction is limited owing to its reduced reproductive potential, that is, it should be multiplied by w . Note that it had already chosen, at some point before reproductive maturity, to develop into an irreversible worker caste (Crespi and Yanega 1995). The net increase of group productivity is denoted as α (> 0), which arises from the staying and helping of the newly evolved worker caste. If a subordinate chooses to develop into an irreversible worker caste, the dominant will react to the decision by either tolerating the presence of the worker caste or ejecting it. Given that transactional models assume that the dominant has full control over breeding, in case the dominant should tolerate the worker caste, it must also readjust the staying incentive that it should concede to the newly evolved worker caste so that the inclusive fitness payoff to the newly evolved worker caste from staying should be only equal to that from dispersing. We denote p' as the staying incentive the newly evolved worker caste would be given, and it may or may not be the same as p .

Our aim is to determine under what conditions a totipotent subordinate being, given the staying incentive in a stable group, will choose to develop into an irreversible worker caste over evolutionary time. Table 1 clarifies the reproductive output for a dominant, a totipotent subordinate, and a newly evolved worker caste according to whether it stays or disperses. We stress that the newly evolved worker caste is still able to disperse should it re-

Table 1: Reproductive outputs for a dominant, a totipotent subordinate, and a newly evolved worker caste in the dyadic transactional skew model

	Subordinate (totipotent subordinate/ worker caste) stays	Subordinate (totipotent subordinate/ worker caste) leaves
Dominant	$k(1 - p_s)$	1
Totipotent subordinate	kp_s	x
Dominant	$(k + \alpha)(1 - p'_s)$	1
Worker caste	$w(k + \alpha)p'_s$	wx

ceive less than its minimum share. We took the following procedure in the entire article.

First, we sought the new staying incentive p' from the viewpoint of the newly evolved worker caste. By comparing the worker caste's option of staying in the group with its option of dispersing, we found out the minimum share of direct reproduction that the newly evolved worker caste should require from the dominant.

Second, we checked out whether the dominant would tolerate the subordinate's decision and concede p' to the newly evolved worker caste, from the dominant's viewpoint. We compared the dominant's option of tolerating the worker caste and donating p' with its option of retaining the original totipotent subordinate.

Third, we determined whether the totipotent subordinate would benefit from developing into a specialized worker caste, from the subordinate's viewpoint. We compared the subordinate's option of becoming a worker caste and receiving p' with its option of remaining as a totipotent subordinate and receiving p .

For the dyadic, symmetrical groups with positive staying incentives (partial skew), we first seek p' by using Hamilton's rule (inequality [1]) from the worker's viewpoint:

$$w(k + \alpha)p' + r(k + \alpha)(1 - p') > wx + r. \quad (3)$$

Solving for p' , we obtain the staying incentive p' :

$$p' = \begin{cases} w > r, & \frac{wx - r(k - 1 + \alpha)}{(k + \alpha)(w - r)} \\ w \leq r, & 0 \end{cases}. \quad (4)$$

When $w > r$, subtracting p' from p yields

$$\frac{r(1 - w)k[(k + \alpha) - (x + 1)] + r\alpha(w - r)}{(1 - r)(w - r)k(k + \alpha)},$$

which is >0 . Also, when $w \leq r$, the new staying incentive p' ($=0$) is smaller than the former staying incentive p . It follows that if a totipotent subordinate develops into an irreversible worker caste, even a staying incentive smaller than the former staying incentive will be good enough for the worker caste to stay in the group. Second, will the

dominant be then favored to donate this staying incentive (eq. [4]) to the newly evolved worker caste? The condition is determined by applying Hamilton's rule (inequality [1]) from the viewpoint of the dominant:

$$(k + \alpha)(1 - p') + rw(k + \alpha)p' > k(1 - p) + rkp. \quad (5)$$

Reflecting on the initial condition that ecological constraints are moderate, that is, $r(k - 1) < x < k - 1$, we can easily see that inequality (5) is always true. In other words, the dominant is always favored to tolerate the totipotent subordinate's decision to become an irreversible worker caste. Third, will the subordinate be willing to develop into a worker caste? We can determine the condition under which the subordinate prefers to become a worker caste rather than remain in the group as a "totipotent" subordinate:

$$w(k + \alpha)p' + r(k + \alpha)(1 - p') > kp + rk(1 - p). \quad (6)$$

Substituting equations (2) and (4) for p and p' in inequality (6), we find the condition as follows:

$$\begin{cases} w > r, & w > 1 \\ w \leq r, & \alpha > \frac{(k - 1)(1 - r)}{r} \end{cases}. \quad (7)$$

When $w > r$, inequality (6) reduces to $w > 1$, which contradicts the assumption that $0 \leq w < 1$. This means that caste differentiation cannot be selected. When $w \leq r$, by comparison, inequality (6) reduces to $x < r(k - 1 + \alpha)$. By the assumption that $r(k - 1) < x < k - 1$, the condition we seek is $\alpha > (k - 1)(1 - r)/r$. This means that when the reproductive potential of the newly evolved worker caste is less than or equal to the genetic relatedness between the two parties, caste differentiation can be selected only if the relatedness is sufficiently high and the net increase in group productivity is sufficiently large. In most cases, however, the reproductive potential of the newly evolved worker caste is most likely to approach 1.0 because we are focusing on the transition from 1.0 to w , and one of the assumptions underlying Hamilton's rule is that selection should be weak (Grafen 1984, 1985). Notice that, should

caste differentiation take place, no staying incentive would be offered to the newly evolved worker caste (see eq. [4]). In short, our model predicts that, in a stable association where the totipotent subordinate is being given the staying incentive, phenotypic caste differentiation into breeder and worker caste will be very unlikely to occur, unless genetic relatedness is extremely high.

*Symmetrical Relatedness, Zero Staying Incentives
(Complete Skew)*

Under strong ecological constraints, that is, $x < r(k - 1)$, the subordinate will remain in the group with no staying incentive. Repeating the procedure of inequality (3), we obtain the new staying incentive p' , which is always 0. Note that when $w > r$, the new staying incentive is greater than $[wx - (k - 1 + \alpha)] / (k + \alpha)(w - r)$, which is negative. This implies that the new staying incentive will be 0. However, by repeating inequality (5) and substituting 0 for p and p' , we obtain $\alpha > 0$, which is true by assumption. The dominant, hence, will always be favored to tolerate the worker caste receiving no staying incentives rather than eject it.

The condition under which a totipotent subordinate will choose to develop into an irreversible worker caste is given by inequality (6). Substituting 0 for p and p' , we obtain $r > 0$. Thus, our model predicts that if and only if the two parties are related, caste differentiation is predicted to occur irrespective of the degree of genetic relatedness. As we shall see, however, caste differentiation in a symmetrical relatedness group exhibiting no staying incentives (complete skew) is far less likely to occur for some other reasons.

Asymmetrical Relatedness (Parent-Offspring Groups)

The transactional skew model predicts that, in a stable group where the subordinate is the offspring of the dominant, the dominant will monopolize reproduction (Reeve and Keller 1995). We obtain the new staying incentive p' by applying Hamilton's rule (inequality [1]) from the subordinate's viewpoint:

$$w(k + \alpha)p' + r_{sd}(k + \alpha)(1 - p') > wx + r_{sd}, \quad (8)$$

where r_{sd} is the relatedness of the subordinate to the dominant's offspring, divided by the subordinate's relatedness to its own offspring. Assuming the dominant mated with a single partner, we find that $r_{sd} = .50/.50 = 1$. By replacing r_{sd} with 1.0 and solving for p' , inequality (8) reduces to

$$p' < \frac{wx - (k - 1 + \alpha)}{(k + \alpha)(w - 1)},$$

which is negative. The new staying incentive p' , hence, becomes 0. Moreover, we can easily see that the dominant will tolerate the caste differentiation by repeating inequality (5), where r is substituted by 1 and both p and p' are substituted by 0.

The condition under which the totipotent subordinate will choose to develop into an irreversible worker caste is given by inequality (6). Substituting 0 for p and p' , we find that $\alpha > 0$, which is always true by assumption. In summary, our model predicts that, in parent-offspring associations where the subordinate is the offspring of the dominant, irreversible divergence into breeder and worker caste should always be favored, no matter how small the net increase of group productivity may be.

**The N-Person Transactional Model of
Caste Differentiation**

*Symmetrical Relatedness, Positive Staying Incentives
(Partial Skew)*

On the basis of the N -person transactional model framework (Reeve 2000; Reeve and Emlen 2000), we explore the condition under which a totipotent subordinate in an arbitrarily sized (N -person) group will choose to develop into a morphological worker caste. Following Reeve and Emlen (2000), we assume that only staying incentives can be given, that the total group productivity $g(N)$ is an increasing concave function of the group size (N), and that the group consists of a single dominant with multiple totipotent subordinates ($N - 1$ individuals). We also assume that if a single totipotent subordinate decides to become a worker caste—that is, its reproductive potential becomes smaller from 1.0 to w —group productivity would increase by the degree α (> 0). If, for instance, all the totipotent subordinates in a group decide to become workers, group productivity would be $g(N) + (N - 1)\alpha$. Reeve and Emlen (2000) labeled the evolutionarily stable size of a group as the “saturated” group size, that is, the maximal stable size above which subsequent joining by subordinates is no longer favored over independent breeding. In terms of this, the subordinate in an N -person group may take into account the decision to become a worker caste only in the saturated groups.

The generalized Hamilton's rule for the N -person skew model is given by

$$\sum_{m=1}^N r_m K_{m,i} > \sum_{m=1}^N r_m K_{m,j}, \quad (9)$$

where N is the group size and m indexes the group number; if s indicates self, $r_s = 1.0$ and $K_{s,i} = P_i$ and $K_{s,j} = P_j$ from the dyadic model. From this, we can obtain the

magnitude of the staying incentive for a subordinate in a group of size N (Reeve and Emlen 2000):

$$p_s(N) = \frac{xg(1) - r[g(N) - g(N - 1)]}{g(N)(1 - r)}, \quad (10)$$

where $xg(1)$, denoted as S , is the expected absolute reproduction of a solitary breeder. However, the condition under which the dominant will be willing to concede the staying incentive rather than eject the subordinate can be also obtained as follows (Reeve and Emlen 2000):

$$\begin{aligned} &g(N)[1 - (N - 1)p_s(N)] \\ &+ r(N - 2)g(N)p_s(N) + rg(N)p_s(N) \\ &> g(N - 1)[1 - (N - 2)p_s(N - 1)] \\ &+ r(N - 2)g(N - 1)p_s(N - 1) + rS. \end{aligned} \quad (11)$$

One can determine the critical value of S at which the left-hand side of the inequality (11) becomes negative, that is, the group reaches its saturated size:

$$S_{\text{crit}} = \frac{[1 + r(N - 1)][g(N) - g(N - 1)] - r(N - 2)[g(N - 1) - g(N - 2)]}{1 + r}. \quad (12)$$

When S is larger than S_{crit} , the dominant is favored to eject the subordinate. Thus, the group is saturated when $S = S_{\text{crit}}$ (Reeve and Emlen 2000).

Under what conditions will a focal totipotent subordinate in an N -person group choose to become an irreversible worker caste? First, the new staying incentive that the worker caste should be given, denoted as $p'_s(N)_c$, is given by Hamilton's rule (eq. [9]) from the worker's viewpoint:

$$\begin{aligned} &w[g(N) + \alpha]p'_s(N)_c + r[g(N) + \alpha][1 - p'_s(N)_c] \\ &> wS + rg(N - 1). \end{aligned} \quad (13)$$

Rearranging inequality (13), we obtain $p'_s(N)_c$:

$$p'_s(N)_c = \begin{cases} w > r, & \frac{wS - r[g(N) - g(N - 1) + \alpha]}{[g(N) + \alpha](w - r)} \\ w \leq r, & 0 \end{cases}. \quad (14)$$

As in the case of the dyadic model, the new staying incentive $p'_s(N)_c$ is always smaller than the former staying incentive $p_s(N)$. When $w > r$, for example, subtracting $p'_s(N)_c$ from $p_s(N)$ yields

$$\frac{r(1 - w)g(N)\{[g(N) + \alpha] - [S + g(N)]\} + r\alpha(w - r)g(N - 1)}{(1 - r)(w - r)g(N)[g(N) + \alpha]}, \quad (15)$$

which is > 0 . Second, we determine the staying incentive all the other $N - 2$ subordinates should be given anew, denoted as $p'_s(N)_t$, after a focal totipotent subordinate turned into a worker caste. Note that the dominant will try to redistribute staying incentive(s) not only for the focal worker but also for other $N - 2$ totipotent subordinates. The $N - 2$ subordinates will be favored to tolerate the presence of the focal worker rather than expel it from the group when

$$\begin{aligned} &[g(N) + \alpha]p'_s(N)_t + rw[g(N) + \alpha]p'_s(N)_c \\ &+ r(N - 3)[g(N) + \alpha]p'_s(N)_t \\ &+ r[g(N) + \alpha][1 - (N - 2)p'_s(N)_t - p'_s(N)_c] \\ &> g(N - 1)p_s(N - 1) + rwS \\ &+ r(N - 3)g(N - 1)p_s(N - 1) \\ &+ rg(N - 1)[1 - (N - 2)p_s(N - 1)], \end{aligned} \quad (16)$$

which is deduced from Hamilton's rule (inequality [9]) from the other $N - 2$ subordinate's viewpoint. Rearranging inequality (16) and solving for $p'_s(N)_t$, one can find $p'_s(N)_t$ as shown below:

$$p'_s(N)_t = \begin{cases} w > r, & \frac{\{[rw(1 - r) + w - r]S + rw(r - 1)[g(N) - g(N - 1) + \alpha] + (r^2 - rw)[g(N - 1) - g(N - 2)]\}}{[(1 - r)(w - r)(g(N) + \alpha)]} \\ w \leq r, & 0 \end{cases}. \quad (17)$$

Third, by employing Hamilton's rule (inequality [9]) from the dominant's perspective, one can show that the dominant will always be willing to yield staying incentives (14) and (17) rather than eject the focal worker caste. The condition is given by

$$\begin{aligned} &[g(N) + \alpha][1 - (N - 2)p'_s(N)_t p'_s(N)_c] \\ &+ rw[g(N) + \alpha]p'_s(N)_c \\ &+ r(N - 2)[g(N) + \alpha]p'_s(N)_t \\ &> g(N - 1)[1 - (N - 2)p_s(N - 1)] \\ &+ rwS + r(N - 2)g(N - 1)p_s(N - 1), \end{aligned} \quad (18)$$

which always holds true. Finally, the condition under which a focal totipotent subordinate is favored to develop into a worker caste is given by applying Hamilton's rule (inequality [9]) from the viewpoint of the focal subordinate:

$$w[g(N) + \alpha]p'_s(N)_c + r[g(N) + \alpha][1 - p'_s(N)_c] > g(N)p_s(N) + rg(N)[1 - p_s(N)]. \quad (19)$$

Substituting equations (10) and (14) for $p_s(N)$ and $p'_s(N)_c$, respectively, in inequality (16), one can find the condition as follows:

$$\begin{cases} w > r, & w > 1 \\ w \leq r, & \alpha > \frac{[g(N) - g(N-1)](1-r)}{r} \end{cases} \quad (20)$$

This means that, when $w > r$, caste differentiation is not favored by selection, since we assumed that $0 \leq w < 1$. When $w \leq r$, caste differentiation is possible only when

$$\alpha > \frac{[g(N) - g(N-1)](1-r)}{r}.$$

That is, when the relatedness is sufficiently high, the net increase in group productivity is sufficiently large, and the focal totipotent subordinate's original contribution to group productivity is sufficiently low. By the same reason in the previous dyadic model, however, w will usually be close to 1.0. It follows that, in an N -person saturated group of symmetrically related relatives, a totipotent subordinate with a saturated staying incentive will not choose to develop into a morphological worker caste unless the symmetrical relatedness is extremely high. This conclusion holds true not only for the focal subordinate but also for all the other $N-2$ subordinates, since if any one of the $N-1$ equivalent subordinates benefits from developing into a worker caste, then all the other subordinates will. In other words, once the condition for caste differentiation has been satisfied, all $N-1$ equivalent subordinates in an N -person saturated group will be favored to develop into worker castes simultaneously.

It would also be interesting to ask whether caste differentiation is possible for a saturated group where all individuals are clonal, that is, the genetic relatedness is 1.0. In this case, the N -person transactional model says that all $N-1$ subordinates will remain in the group with no staying incentive. From equation (14), the new staying incentive $p'_s(N)_c$ is also 1.0. Repeating inequality (19) and replacing $p_s(N)$ and $p'_s(N)_c$ with 0, one can readily identify that the condition under which a focal totipotent subordinate in a clonal group is $\alpha > 0$, which is always true by

assumption. Thus, if a saturated group consists of genetically identical individuals, caste divergence is expected to occur.

Symmetrical Relatedness, Zero Staying Incentives (Complete Skew)

According to Reeve and Emlen (2000), the condition for complete skew is $S < r[g(N) - g(N-1)]$, and groups with complete skew would be unsaturated with subordinates "because the dominant will yield staying incentives to subordinates whenever $S < S_{\text{crit}} \approx g(N) - g(N-1)$, that is, at group sizes larger than the maximum size at which complete skew occurs ($S = r[g(N) - g(N-1)]$)." Indeed, this prediction converges on the theoretical argument of a previous study that complete skew is much less likely to occur in symmetrical than in asymmetrical relatedness groups; a survey of both invertebrate and vertebrate societies supported the argument (Reeve and Keller 1995).

Earlier we argued that subordinates in a group would consider developing into morphological worker castes only after the group reaches its saturated size, the evolutionarily stable group size suggested by Reeve and Emlen (2000). For the case of symmetrical relatedness groups, even if groups with complete skew command an absolute majority in a population (e.g., because of severe ecological constraints), a few groups in the population could nonetheless exhibit partial skew in case they confront, unlike other groups, relatively moderate ecological constraints. Recall that complete skew is just one pattern of reproductive partitioning among group members, and it is predicted to change always into partial skew provided that ecological constraints on independent reproduction have decreased (Reeve and Emlen 2000). Taking into account that no external force would keep each and every group in a population exhibiting only complete skew for a long evolutionary time and that Hamilton's rule, when it applies to altruism, is about the spread of a gene causing altruism in the gene bearers through the whole population (Bourke and Franks 1995), we find that caste differentiation is essentially impossible in the unsaturated, symmetrical relatedness groups with complete skew. In other words, we should take a look at saturated, symmetrical groups with partial skew in order to ascertain whether sterile castes could originate in symmetrical relatedness groups. Note that this conclusion contrasts sharply with Keller and Reeve's former assertion (1994, 1998) that the ultimate factors driving caste differentiation are fundamentally the same as those favoring high skew. It should also be noted that an apparently unusual prediction that caste differentiation is possible in the case of two-person symmetrical relatedness groups resulted from the fact that we had unrealistically assumed group size to be fixed at two.

Asymmetrical Relatedness (Parent-Offspring Groups)

For asymmetrical relatedness groups where the subordinates are all offspring of the dominant parent(s), the N -person transactional model predicts that the dominant will monopolize reproduction. The saturated group size, N^* , for parent-offspring groups is determined by the condition $S = g(N^*) - g(N^* - 1)$ (Reeve and Emlen 2000). To begin with, we can see that even if the focal subordinate with no staying incentive decided to become a worker, the new staying incentive it should be given will still be zero because subordinates in a parent-offspring group can never benefit from staying incentives (Reeve and Emlen 2000). By the same token, the other $N - 2$ subordinates would not be given any staying incentive either, should the focal totipotent subordinate become a worker. By applying Hamilton's rule (eq. [9]) from the worker's viewpoint, we can show that the newly developed worker caste with no staying incentives will be favored to remain in the group rather than breed solitarily if

$$\begin{aligned}
 & w[g(N) + \alpha]p'_s(N)_c \\
 & + \left(\frac{1}{2}\right)(N - 2)[g(N) + \alpha]p'_s(N)_t \\
 & + (1)[g(N) + \alpha][1 - (N - 2)p'_s(N)_t - p'_s(N)_c] \quad (21) \\
 & > wS + \left(\frac{1}{2}\right)(N - 2)g(N - 1)p_s(N - 1) \\
 & + (1)g(N - 1)[1 - (N - 2)p_s(N - 1)].
 \end{aligned}$$

Note that the focal totipotent subordinate is related to itself by 1.0, to its siblings by one-half, and to the dominant effectively by 1.0. By substituting 0 for $p'_s(N)_c$, $p'_s(N)_t$, and $p_s(N - 1)$, we reduce inequality (21) to

$$S < \frac{g(N) - g(N - 1) + \alpha}{w} \quad (22)$$

From Hamilton's rule (inequality [9]), it can also be shown that the dominant will be favored to retain the worker caste with no staying incentive rather than eject it if

$$S < \frac{2[g(N) - g(N - 1) + \alpha]}{w}, \quad (23)$$

which always holds true if inequality (22) is true. Hence, the saturated group size in the N -person parent-offspring group containing a single worker caste is simply determined by the condition $S = [g(N^*) - g(N^* - 1) + \alpha]/w$, which is derived from inequality (22). Let us identify whether the focal totipotent subordinate will indeed be favored to develop into a worker caste rather than remain

the group as an ordinary subordinate. From Hamilton's rule (inequality [9]), the condition is given by

$$\begin{aligned}
 & w[g(N) + \alpha]p'_s(N)_c \\
 & + \left(\frac{1}{2}\right)(N - 2)[g(N) + \alpha]p'_s(N)_t \\
 & + (1)[g(N) + \alpha][1 - (N - 2)p'_s(N)_t - p'_s(N)_c] \quad (24) \\
 & > g(N)p_s(N)(N) + \left(\frac{1}{2}\right)(N - 2)g(N)p_s \\
 & + (1)g(N)[1 - (N - 1)p_s(N)].
 \end{aligned}$$

By substituting 0 for $p_s(N)$, $p'_s(N)_c$, and $p'_s(N)_t$, we find that inequality (24) reduces to $\alpha > 0$, which always holds true by assumption. As in the N -person symmetrical relatedness groups, this conclusion applies to all the other $N - 2$ subordinates as well as the focal subordinate. That is, once appropriate conditions are met, all $N - 1$ subordinates in an N -person saturated group with asymmetrical relatedness will be favored to develop into worker castes simultaneously. Also, the saturated group size in the N -person parent-offspring group containing $N - 1$ worker castes is determined by the same condition, $S = [g(N^*) - g(N^* - 1) + \alpha]/w$.

Note that through caste differentiation the critical value of S , S_{crit} , has increased from $g(N^*) - g(N^* - 1)$ to $[g(N^*) - g(N^* - 1) + \alpha]/w$. This means that, if the S value remains constant, since $S_{crit} > S$, some subordinates would be willing to remain in the group that otherwise would leave the group voluntarily (Reeve and Emlen's model [2000] predicts that, in the case of N -person parent-offspring groups, exceeding the saturated group size results in voluntary departure, not eviction, of subordinates). Consequently, our model predicts that caste differentiation in a saturated parent-offspring group will increase its group size in proportion to the net increase of group productivity ($= \alpha$) and the loss of reproductive potential of a worker caste ($= 1 - w$).

It is also easy to show that as the reproductive potential of worker castes becomes less—that is, reproductive division of labor becomes conspicuous—the saturated group size of the group to which the worker castes belong will become larger. Let us assume that $0 \leq w_2 < w_1 < 1$ and $0 < \alpha_1 < \alpha_2$, where w_1 and w_2 correspond to α_1 and α_2 , respectively. Repeating the same procedure as above, we obtain the condition where a weakly altruistic worker caste whose reproductive potential is relatively high ($= w_1$) will be favored to develop into a strongly altruistic worker caste whose reproductive potential is relatively low ($= w_2$):

$$S < \frac{g(N) - g(N-1) + \alpha_2}{w_2}, \quad (25)$$

from which we can readily see that its S_{crit} is again larger than the former value of S_{crit} ($= [g(N^*) - g(N^* - 1) + \alpha_1]/w_1$) by assumption. Thus, saturated group size N^* becomes larger as the reproductive potential of worker castes becomes smaller and the resulting net increase of group productivity becomes larger.

It is not necessary for all offspring in a group to be full siblings, after all. Some factors like extrapaternity can decrease a subordinate's average relatedness to the dominant parent's offspring (relative to its relatedness to its own offspring) to a value < 1 . If, to the extreme degree, all offspring are half-siblings to each other, the value becomes one-half. Thus, inequality (24) should be modified so that the focal subordinate's average relatedness to the dominant's offspring is r instead of 1 and its average relatedness to the other subordinates' offspring (relative to its relatedness to its own offspring) is $r/2$ instead of one-half (Reeve and Emlen 2000). One can easily find that the condition for caste differentiation in this case is also $\alpha > 0$, which always holds true by assumption. However, the saturated group size is determined by a different condition:

$$S < \frac{r[g(N) - g(N-1) + \alpha]}{w}. \quad (26)$$

Compared with inequality (22), this means that although caste differentiation in a saturated parent-offspring group including some proportion of half-siblings does also increase its group size, the amount of increase reduces as the frequency of half-sibling rises, that is, average relatedness among offspring decreases.

Discussion

To our knowledge, our model is the first attempt to investigate explicitly, within the framework of reproductive skew, the ultimate factors that direct individuals to commit themselves developmentally to become workers (see Crespi and Ragsdale 2000 for related discussions). Contrary to prior expectations that caste differentiation should be favored to evolve in situations where skew is very high (Keller and Reeve 1994, 1998), our analysis reveals that the ecological and genetic conditions for the origin of sterile castes are far more restrictive than previously thought. On the assumption that a totipotent subordinate in a group can raise its group productivity by developing into a morphologically specialized worker caste at the cost of a part of its reproductive potential, combining the dyadic with

the N -person skew model for caste differentiation yields the following predictions.

First, for saturated, symmetrical relatedness groups with partial skew, caste differentiation into breeder and worker castes will be virtually impossible, unless symmetrical relatedness is greater than the reduced reproductive potential of worker castes.

Second, if and only if symmetrical relatedness is greater than the reduced potential of worker castes, totipotent subordinates in a saturated, symmetrical relatedness group with partial skew might be favored to develop into worker castes, provided that the net increase of group productivity is sufficiently large and that each totipotent subordinate's original contribution to group productivity is sufficiently low.

Third, if genetic relatedness among saturated, symmetrical relatedness group members is 1.0, then caste differentiation into breeder and worker castes is expected to occur.

Fourth, for unsaturated, symmetrical relatedness groups with complete skew, caste differentiation into breeder and worker castes will not occur.

Fifth, for saturated, asymmetrical relatedness (parent-offspring) groups with complete skew, caste differentiation into breeder and worker castes is expected to occur regardless of the frequency of half-siblings, provided that all subordinates are the dominant's genetic offspring.

Sixth, caste differentiation in a saturated, parent-offspring group with complete skew will increase its saturated group size in proportion to the net increase of group productivity and the loss of reproductive potential of worker castes.

Seventh, as the reproductive potential of worker castes becomes less—that is, reproductive division of labor becomes more conspicuous—the saturated size of the group to which the worker castes belong will become larger.

Subsociality as a Pathway to Eusociality

Why does our model posit that sterile castes may not originate in symmetrical relatedness groups unless the genetic relatedness among group members is extremely high? It seems counterintuitive, since the prediction remains the same regardless of the net increase of group productivity, the severity of ecological constraints, and the magnitude of symmetrical relatedness (on the condition that it should not exceed the reduced reproductive potential of worker castes). The answer is that, even if a totipotent subordinate is able to increase group productivity remarkably by developing into a worker caste, the dominant will react to the subordinate by reducing the staying incentive the subordinate should be given anew as a worker caste, as long as the newly evolved worker caste prefers staying in the

group to breeding solitarily. One can easily identify that the new staying incentive is inversely proportional to the net increase of group productivity, the prospect of independent breeding, and symmetrical relatedness (see eqq. [4], [14]). If the totipotent subordinate were to become a specialized worker caste, its inclusive fitness would never increase because of the dominant's conceding the minimum share of reproduction just enough to prevent the newly evolved caste from dispersing. So the focal totipotent subordinate in a symmetrical relatedness group may not choose to develop into a worker caste.

By contrast, our analysis predicts that caste specialization would evolve in parent-offspring groups regardless of the frequency of half-siblings, provided that all subordinates are the dominant's genetic offspring. The focal subordinate in this situation will receive no staying incentives whether or not it decides to become a worker caste. Its inclusive fitness payoff, therefore, depends on only its indirect fitness component, which can be augmented as much as the net increase of group productivity if only it decides to become a worker caste. The same is true of saturated, symmetrical relatedness groups with partial skew where the relatedness is greater than the reduced potential of worker castes.

These predictions have profound implications for the old argument about whether eusociality evolved through a subsocial or a semisocial pathway, that is, whether worker castes arose from offspring in parent-offspring associations or individuals in single-generation associations (we here adopt Crespi and Yanega's [1995] definition of eusociality as the presence of alloparental care and permanent caste differentiation; Michener 1969; Wilson 1971; Lin and Michener 1972; Alexander et al. 1991; Seger 1991). Alexander et al. (1991) asserted that the contrasting of subsociality and semisociality in the argument may have been misleading because all of the so-called semisocial species are also already subsocial, that is, showing parental care. They argued that phenotypic divergence into breeder and worker castes in single-generation associations is unlikely because of the lack of reproductive head start advantage of workers (Queller 1989); the cost of added time and risks in mating and colony founding; various uncertainties such as mortality during dispersal, nest founding, and/or overwintering; and the relative genetic disadvantage of helping to nieces and nephews compared with helping to sibs (Bourke and Franks 1995). Our analysis implies that the last genetic reason, in particular, may have played a vital role in the evolution of eusociality. Indeed, it has occasionally been suggested that relatedness asymmetry in parent-offspring associations causes an offspring subordinate to be neutral about how much direct reproduction it receives from the dominant parent so that this situation

forms the basis of eusociality (Charnov 1978; Stubblefield and Charnov 1986; Reeve and Keller 1995).

Much evidence seems to support the above predictions. Aside from some clone-forming species, most or all eusocial species having morphological castes are composed of parent(s) and a number of its/their offspring. Examples include some thrips with soldiers (Crespi 1992; Crespi and Mound 1997), fungus ants (*Atta* spp.; Hölldobler and Wilson 1990), honeybees (*Apis mellifera*; Seeley 1985), mound-building termites (*Macrotermes* spp.; Shellman-Reeve 1997), yellow jacket wasps (*Vespa* spp.; Greene 1991), and naked mole rats (*Heterocephalus glaber*; O'Rian et al. 1996, 2000; Braude 2000). On the contrary, we know of no instances of the existence of phenotypic worker castes within single-generation associations where helpers assist same-age/older siblings or nieces and nephews using their specialized morphology. For example, it is widely known that plurimatrous (sensu Choe 1995), or multiple-queen, colonies are common in social insects, especially among ants. To our knowledge, however, morphological specialization among coexisting queens has never been reported (Keller 1993, 1995; Bourke and Heinze 1994). Our model predicts that, if such evidence is found, the symmetrical relatedness in that case (r) should be so high as to exceed the reduced reproductive potential of workers (w), the net increase of group productivity due to worker's specialized morphology (α) should be sufficiently large, and each totipotent subordinate's original contribution to group productivity should be sufficiently low. Thus, such cases will offer a valuable opportunity to test critically our model, although we still believe that they may be very rare in nature. One might suspect that, in the first stage of transition from 1.0 to w , w could be markedly <1.0 in case a mutation involving relatively large reductions in reproductive potential has occurred. This objection, however, fails to take into account that Hamilton's rule is based on the assumption of weak selection (Grafen 1984, 1985). The assumption is reasonable since, when natural selection is "fine-tuning" a character, the only relevant selection pressures are weak ones; strong ones act only on heavily disadvantageous mutants (Grafen 1985; Hamilton 1996). The fundamental Darwinian principle, too, depends on fine-tuning under weak selection, which enables the precise optimum to evolve.

In support of the third prediction, morphologically specialized castes have also been known in a few clone-forming species, such as some aphids with soldiers (Aoki 1987; Stern and Foster 1997) and polyembryonic wasps (Cruz 1981). For example, the broods of a parasitoid wasp, *Copidosoma floridanum*, proliferate clonally up to some 1,200 embryos in a host. A few of the embryos function as a sterile soldier caste that defends other reproductive siblings from competitors (Harvey et al. 2000).

Interestingly, our result suggests that, in the case of (diploid) parent-offspring groups, unusually high relatedness between altruistic workers and recipients is not necessary for explaining the origin of specialized worker castes; the normal degree of relatedness found in any family of parents and offspring ($r = 0.5$) will be sufficient (the fifth prediction), without regard to the frequency of half-sibs (of course, this does not rule out the possibility that the high level of genetic relatedness in parent-offspring groups could nonetheless facilitate the origin of sterile castes; this is beyond the scope of this article, however). Recent data investigating the effect of genetic relatedness in diploid eusocial species provide support for our models. Despite many attempts to demonstrate some genetic effects in termites that might mimic the influence of haplodiploidy on Hymenopteran relatedness levels (e.g., Hamilton 1972; Bartz 1979; Luykx and Syren 1979; Lacy 1980), current analyses using multilocus DNA fingerprinting or allozymes have shown that the within-colony relatedness level in termites is no greater than 0.5 (Reilly 1987; Thompson and Hebert 1998; Husseneder et al. 1999). Similarly, it has also been believed that unusually high relatedness within colonies arising from extreme inbreeding could explain the eusociality of naked mole-rats (Faulkes et al. 1990; Reeve et al. 1990; Sherman et al. 1992; Jarvis et al. 1994). Recent studies suggest, however, that inbreeding is not the mode of mating in this species and that outbreeding is probably frequent; the limited genetic variation found in earlier molecular genetic studies probably resulted from a population bottleneck and recent common ancestry (O'Riain et al. 1996; Braude 2000; Ciszek 2000).

Integrating Group Size with Reproductive Skew

According to our analysis, phenotypic divergence into breeder and worker castes in parent-offspring groups is expected to occur no matter how small the group size is. But it is well known that, with the possible exception of naked mole rats, there are no morphologically specialized worker castes in cooperative breeding vertebrates, accounting roughly 3% of bird and mammal species (Emlen 1997). The apparent discrepancy disappears, however, by incorporating the possibility of subordinates inheriting the dominant's breeding status (and hence control over local resources) in the future (Kokko and Johnstone 1999; Ragsdale 1999). When the caste differentiation model is extended to include resource inheritance, one can find that the condition under which phenotypic divergence is favored is not $\alpha > 0$, which is always true by assumption, but $\alpha > (1 - w)i$; that is, the net increase of group productivity should be sufficiently large, the reduced reproductive potential should be sufficiently high, and the re-

source inheritance i (sensu Ragsdale 1999) should be sufficiently small (see appendix).

In hypothetical ancestral situations, the two parties of a dyadic group would have the same life span; further, no competitors would hinder the subordinate. Thus, the probability of inheriting the dominant's breeding status in this case may be quite high, which means that i may also be very high and that it will be very hard for the condition for caste differentiation, $\alpha > (1 - w)i$, to be satisfied. Yet as group size increases because of various ecological pressures, the increased number of competitive subordinates decreases the probability of a particular subordinate acquiring dominant status until the condition for caste differentiation is met (Shreeves and Field 2002). Put another way, a totipotent subordinate living in a parent-offspring group where the group size has reached a certain critical point may transmit its genes more efficiently by developing into a morphological worker caste at the cost of a part of its reproductive potential than by retaining its full reproductive potential and waiting for the dominant's death.

One of the main findings of our model is that caste differentiation in a parent-offspring group increases its saturated group size. Also, the positive interaction between group size and the degree of caste differentiation can continue in principle until totally sterile worker castes emerge. Hence, at least in parent-offspring groups where an irreversible specialization for helping can be selected, group size may be a good indicator of the level of social complexity. In fact, group size has already been referred to as one of the key factors of social complexity (Wilson 1971; Michener 1974; Hölldobler and Wilson 1990; Alexander et al. 1991; Tschinkel 1991; Sherman et al. 1995; Bourke 1999; Johnstone 2000). However, group size has attracted less attention than other factors such as kin structure, perhaps because it is difficult to demonstrate that its association with social complexity is not a mere correlation but a genuine causation. Bourke (1999) recently compiled abundant evidence that group size, the reproductive potential of workers, and the degree of caste differentiation are bound together by feedback loops of mutual reinforcement, and he argued that group size should deserve to be a major determinant of social complexity. In that our caste differentiation model based on reproductive skew framework has reached essentially the same conclusion as Bourke's (1999), we envision a truly unified theory of social evolution in which the subject of the evolution of sterile castes is not bound to any one dimension, be it the degree of reproductive skew or group size.

We present a possible scheme for such a unified framework of social evolution (fig. 1). In the case of two-person parent-offspring groups, the condition for caste differentiation, $\alpha > (1 - w)i$, is quite difficult to meet, as discussed above. As group size increases, i decreases until it pays for

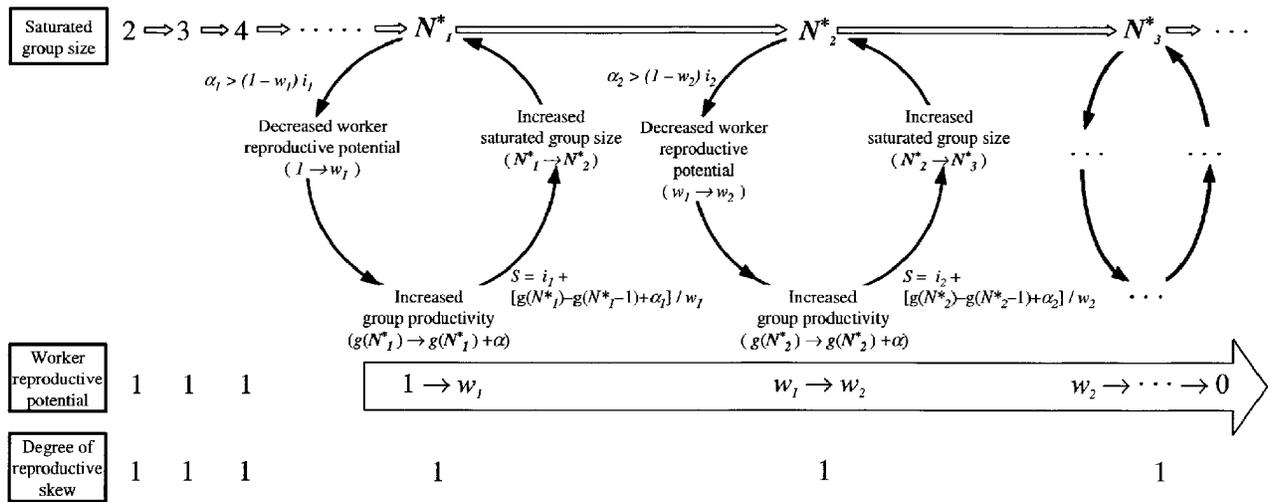


Figure 1: Schematic diagram for the evolution of sterile worker castes that integrates the role of group size into the framework of reproductive skew theory. Note that it applies only to parent-offspring groups with complete skew. We do not consider the probability of “peace incentives” (Reeve and Ratnieks 1993). The probability of resource inheritance (Ragsdale 1999) is taken into account.

a focal totipotent subordinate to develop into a specialized worker caste. Once the condition for caste differentiation, $\alpha_1 > (1 - w_1) i_1$, is satisfied, all totipotent subordinates will simultaneously choose to develop into morphologically specialized worker castes, and they will accordingly increase group productivity by the amount α_1 . Note that the reason for the newly evolved worker castes to stay in the group and help the dominant parent is that it is still in each worker’s interest to do so rather than breed solitarily with its reduced reproductive potential. Since the saturation size of parent-offspring groups is determined solely by the voluntary departure of subordinates (Reeve and Emlen 2000), rising group productivity enables more subordinates to choose to stay in the group, as reflected in

$$S_{\text{crit}} = i_1 + \frac{g(N_1^*) - g(N_1^* - 1) + \alpha_1}{w_1}.$$

Group size has increased from N_1^* to N_2^* , decreasing further the value of resource inheritance from i_1 to i_2 . Accordingly, the condition for further caste differentiation, $\alpha_2 > (1 - w_2) i_2$, is more likely to be met, and then the next feedback loop of caste differentiation, group productivity, and group size will operate. In sum, the viewpoint emphasizing the role of group size in the evolution of eusociality is nicely integrated in the framework of reproductive skew theory.

Growing evidence already points out that, in many societies where partially or completely sterile worker castes

exist, the mature group size is associated with reproductive potential of workers and the degree of caste differentiation (e.g., see tables 1 and 2 in Bourke 1999). This is also in accord with our sixth and seventh predictions. For instance, there exists a significant positive association between colony size and the degree of queen-worker size dimorphism in 14 species and subspecies of Japanese vespine wasps (Matsuura and Yamane 1990; Bourke 1999). Moreover, the only eusocial vertebrate species with morphological caste differentiation, the naked mole rat (O’Riain et al. 1996, 2000; Ciszek 2000), has the largest average group size (around 70–80) in the African naked mole rats (Faulkes et al. 1997; Lacy and Sherman 1997). In contrast, the Damaraland mole rat (*Cryptomys damarensis*) with no morphological caste divergence lives in colonies averaging 16 individuals (Jarvis and Bennett 1993). In view of our models, only naked mole rats seem to have just passed over the critical group size (N_1^* in fig. 1), at which point it is in subordinates’ interests to develop into morphologically specialized workers.

Our caste differentiation model can be readily tested by examining the relationship between the saturated group size and the extent of reduced reproductive potential ($1 - w$). The model predicts that there should be a positive correlation between the two variables if other confounding factors hold constant. It will be interesting, hence, to investigate a suitable taxonomic group exhibiting a wide range of morphological caste specialization and various group sizes. For instance, in the phylogenetically primitive

ants Ponerinae (~1,300 species), many species show a limited queen-worker dimorphism and relatively small colony sizes ($10 \sim 10^3$ adults), whereas some species do show a marked dimorphism and large colony sizes (Peeters 1993, 1997). Comparative studies of Ponerinae have shown that queen fecundity, estimated by the number of ovarioles in queens, is positively correlated with colony size (Peeters 1987; Villet et al. 1991; Peeters and Ito 2001). We speculate that the extent of reduced reproductive potential ($1 - w$) may be inferred by the ratio of the number of worker's ovarioles to queen's ones; therefore, examining its relationship with group size in Ponerinae would be a sensitive test of our model. Another revealing test of our model will be a comparison of mature group size between populations of a single species or among closely related species where average relatedness among offspring varies and cast divergence has occurred. Our model predicts that, all else being equal, the saturated group size will be positively correlated with the level of average relatedness among offspring.

An intriguing comparison can be made between Crespi and Ragsdale's (2000) manipulation model and our caste differentiation model. They argued that manipulation by dominants should be particularly common in parent-offspring groups because of parents' intrinsic advantages over offspring, such as those with age and experience. In view of this, the familiar phenomenon in Hymenoptera that the amount of food fed to the larvae determines offspring size and sometimes caste has been suggested as a good example of manipulation by dominants. As Crespi and Ragsdale (2000) admitted, however, if manipulation occurs, subordinates may be counterselected to resist it (Seeley 1985; Keller and Nonacs 1993). Further, even if certain manipulative acts like parents' underfeeding of their offspring could preempt such resistance and thus induce the origin of morphological castes, the fact still remains that offspring's loss of totipotency has never occurred in the whole cooperative breeding birds and occurred only once in mammals. We believe that all these phenomena in nature can be more adequately explained by our caste differentiation model; that is, whether a totipotent subordinate develops into a specialized worker caste entirely depends on the subordinate's decision to increase its own inclusive fitness. In case of most vertebrate societies, their relatively small group size would make the value of resource inheritance, i , too high for the condition for caste differentiation, $\alpha > (1 - w)i$, to be met.

Conclusions and Prospects

Overall, our caste differentiation model based on the transactional framework seems to provide many interesting predictions, most of which are well supported by existing data.

High or even complete skew does not guarantee the origin of specialized worker castes. At least in parent-offspring groups forming most of well-organized societies in nature, not the degree of reproductive skew but group size functions as the key factor driving the evolution of social complexity.

The degree of reproductive skew in social groups has been regarded as directing the evolution of many key social attributes such as within-group conflict (Reeve and Ratnieks 1993; Reeve 2000), task specializations (Reeve and Ratnieks 1993), resource sharing (Tibbetts and Reeve 2000), and morphological caste differentiation (Sherman et al. 1995). Our model clearly demonstrates that caste differentiation cannot be determined by the degree of reproductive skew alone; unlike other key social attributes, it requires very specific and limited combinations of genetic, ecological, and social factors as well. In view of this, our results may support Crespi and Yanega's (1995) view that caste differentiation among group members indicates that selection pressures on social groups have transformed radically. However, given that the evolution of sterile castes is still depicted in our scheme as a continuous decrease of worker reproductive potential, our results may not fundamentally deviate from the view of Sherman et al. (1995). Considering that the two contrasting views all consent that partitioning of reproduction in social groups provides the fundamental basis to investigate the common selective principles underlying both vertebrate and invertebrate societies, they are actually more compatible than they appear (Crespi and Choe 1997b).

What we disagree with is simply the notion that only the skew value can serve as a useful heuristic for taxonomic comparisons of social evolution (Sherman et al. 1995); any single skew index could lump together radically different reproductive phenomena (Nonacs 2000; as shown in fig. 1, the degree of reproductive skew in parent-offspring groups is theoretically always 1.0 whether irreversible castes evolve or not). That skew value alone cannot tell us the presence of castes and/or the level of social complexity in a given social group does not necessarily mean that reproductive skew theory is inadequate to explain the evolution of sterile worker castes. Far from it, we here showed that even a possible answer to the famous question of Darwin, the origin of sterile castes, could be completely deduced from the transactional skew framework. All social systems could be ultimately arranged along a continuum, but the continuum would be more complex and rather different from what has been thought. Our analysis suggests that the continuum would include the origin of sterile castes as an evolutionarily important event by which selection pressures on social group have been qualitatively and quantitatively changed. In conclusion, our application of skew theory to the origin of sterile castes substantially

extends the scope of the theory to situations where not all individuals are totipotent, and thus it provides a theoretical bridge to the evolution of complex societies.

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APPENDIX

Caste Differentiation Model That Incorporates the Future Direct Reproduction of Subordinates

In this article, we adopt Ragsdale’s (1999) approach that a (potential) subordinate joining a dominant individual will enjoy a resource inheritance, i , as well as staying incentives yielded by the dominant (as before, we do not consider “peace incentives”). Ragsdale (1999) defined the resource inheritance i as the probability of inheriting valuable resources multiplied by the expected number of offspring that an individual would produce after it inherits the resources (relative to a lone breeder). If the subordinate chooses to develop into an irreversibly specialized worker caste, the worker caste will enjoy the resource inheritance wi instead of i .

For two-person parent-offspring groups, the new staying incentive p' that the subordinate will receive is given by modifying inequality (8):

$$[w(k + \alpha)p' + wi] + 1(k + \alpha)(1 - p') > wx + 1. \tag{A1}$$

Inspection of inequality (26) reveals that the new staying incentive p' is 0. The condition under which the dominant will allow the worker caste with no staying incentives to stay in the group rather than eject it is given by modifying inequality (5):

$$(k + \alpha)(1 - p') + \left(\frac{1}{2}\right)[w(k + \alpha)p' + wi] > k(1 - p) + \left(\frac{1}{2}\right)(kp + i). \tag{A2}$$

By replacing p and p' with 0, we reduce inequality (A1) to $\alpha > (1/2)(1 - w)i$. However, the condition where a totipotent subordinate will develop into a worker caste rather than stay in the group as a totipotent subordinate is given by modifying inequality (6):

$$[w(k + \alpha)p' + wi] + (k + \alpha)(1 - p') > (kp + i) + k(1 - p). \tag{A3}$$

By replacing p and p' with 0, we reduce inequality (A2) to $\alpha > (1 - w)i$. Hence, whether irreversible worker castes evolve is solely determined by the totipotent subordinate’s decision, $\alpha > (1 - w)i$; the net increase of group productivity should be sufficiently large, the reduced reproductive potential should be sufficiently high, and the resource inheritance should be sufficiently small.

For N -person parent-offspring groups, the newly developed worker caste with no staying incentives will be favored to remain in the group rather than breed solitarily if

$$\begin{aligned} & \{w[g(N) + \alpha]p'_s(N)_c + wi\} + \left(\frac{1}{2}\right)(N - 2)\{[g(N) + \alpha]p'_s(N)_t + i\} + (1)[g(N) + \alpha][1 - (N - 2)p'_s(N)_t - p'_s(N)_c] \\ & > wS + \left(\frac{1}{2}\right)(N - 2)[g(N - 1)p_s(N - 1) + i] + (1)g(N - 1)[1 - (N - 2)p_s(N - 1)]. \end{aligned} \tag{A4}$$

By substituting 0 for $p'_s(N)_c$, $p'_s(N)_v$, and $p_s(N-1)$, we reduce inequality (A3) to

$$S < \left[\frac{g(N) - g(N-1) + \alpha}{w} \right] + i \quad (\text{A5})$$

It is also easy to show that the dominant will be favored to retain the worker caste receiving no staying incentive rather than eject the worker caste if

$$S < \left\{ \frac{2[g(N) - g(N-1) + \alpha]}{w} \right\} + i, \quad (\text{A6})$$

which always holds true if inequality (A4) is true. Hence, the saturated group size in this case is determined by the condition

$$S = i + \left[\frac{g(N^*) - g(N^* - 1) + \alpha}{w} \right],$$

which is derived from inequality (A4). This result is intuitively understood, since if there is additional probability of resource inheritance, then the more worker castes will remain in the group. The condition where the focal totipotent subordinate will be favored to develop into a worker caste versus to remain in the group as an ordinary subordinate is given by modifying inequality (24):

$$\begin{aligned} & \{w[g(N) + \alpha]p'_s(N)_c + wi\} + \left(\frac{1}{2}\right)(N-2)\{[g(N) + \alpha]p'_s(N)_t + i\} + (1)[g(N) + \alpha][1 - (N-2)p'_s(N)_t - p'_s(N)_c] \\ & > [g(N)p_s(N) + i] + \left(\frac{1}{2}\right)(N-2)[g(N)p_s(N) + i] + (1)g(N)[1 - (N-1)p_s(N)]. \end{aligned} \quad (\text{A7})$$

By substituting 0 for $p_s(N)$, $p'_s(N)_c$, and $p'_s(N)_v$, we reduce inequality (24) to $\alpha > (1-w)i$. It is also worth noting that, in the case of symmetrical relatedness groups, the probability of resource inheritance makes it much more difficult for specialized worker castes to evolve.

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