PARTITIONING OF REPRODUCTION IN MOTHER-DAUGHTER VERSUS SIBLING ASSOCIATIONS: A TEST OF OPTIMAL SKEW THEORY

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Abstract.—A critical feature of cooperative animal societies is the reproductive skew, a shorthand term for the degree to which a dominant individual monopolizes overall reproduction in the group. Our theoretical analysis of the evolutionarily stable skew in matrilineal (i.e., mother-daughter) societies, in which relatednesses to offspring are asymmetrical, predicts that reproductive skews in such societies should tend to be greater than those of semisocial societies (i.e., societies composed of individuals of the same generation, such as siblings), in which relatednesses to offspring are symmetrical. Quantitative data on reproductive skews in semisocial and matrilineal associations within the same species for 17 eusocial Hymenoptera support this prediction. Likewise, a survey of reproductive partitioning within 20 vertebrate societies demonstrates that complete reproductive monopoly is more likely to occur in matrilineal than in semisocial societies, also as predicted by the optimal skew model.

A critical feature of animal societies is the reproductive skew, a shorthand term for the distribution of direct reproduction among individuals (including potentially reproductive nonbreeders) (Vehrencamp 1983a, 1983b). In high-skew societies, actual direct reproduction is concentrated in one or a few dominant individuals in the colony; in low-skew societies, reproduction is distributed more evenly among individuals.

This degree of reproductive skew can be quantified as $(N_b \times v + N_n)/(N_b + N_n)$, where $N_b$ is the number of breeders in the group, $N_n$ is the number of nonbreeders in the group, and $v$ is a standardized measure of the variation in reproduction among breeders. When there is a single breeder, $v$ is defined to be one; when there are multiple breeders, $v$ is defined as the observed variance among breeders in the proportion of total reproductive offspring produced, divided by the maximum possible value for this variance (Keller and Vargo 1993; Reeve and Ratnieks 1993). In the latter case, $v$ is equal to $N_b s^2$, where $s^2$ is the sample variance in the proportion of total offspring produced by breeders (i.e., $s^2 = [\sum (p_i - 1/N_b)^2]/[N_b - 1]$, where $p_i$ is the proportion of all offspring produced by the $i$th breeder). This index of reproductive skew is designed to vary between zero and one. When a single individual produces all the offspring, the skew is one; when
reproduction is perfectly equitable among all group members, the skew is zero. When the dominant breeder yields reproduction to the subordinate as an inducement to stay at the nest and cooperate peacefully, that is, when there is a "social contract" over reproduction (Reeve and Nonacs 1992), the degree of skew is predicted to influence other key attributes of societies, such as the frequency and intensity of dominance interactions and the division of labor within colonies (Reeve 1991; Reeve and Ratnieks 1993). For example, when a subordinate of a given fighting ability receives a smaller fraction of the overall reproduction (i.e., the skew is higher), the subordinate should be more likely to aggressively "test" the dominant's strength, because the subordinate stands to inherit the large skew if a reversal in dominance occurs. (If there is pure interference competition and no social contract, aggressive interactions may cause the degree of skew, instead of being caused by it; if so, there could be a negative, rather than a positive, correlation between subordinate aggression and the degree of skew.) Thus, an understanding of the ultimate factors controlling reproductive skew may enhance our ability to explain and predict the occurrences of different kinds of societies in different ecological and genetic settings.

Previous models of the evolution of reproductive skew have analyzed how ecological constraints on solitary founding, relatedness of potential breeders, and productivity advantages of peaceful association should influence the evolutionarily stable reproductive skew in animal groups (Vehrencamp 1983a, 1983b), including social insects that have the option to nest alone, join a queen, or usurp a queen (Reeve 1991). Recently these models were extended by examining how relative fighting ability among social insect queens will interact with the above factors to influence the reproductive skew (Reeve and Ratnieks 1993). The general conclusions of these models are that the skew should increase (i.e., reproduction should become less equitable) as the relatedness between dominants and subordinates increases, the probability of successful solitary nest foundation by the subordinate decreases (i.e., for stronger ecological constraints), the subordinate's contribution to colony productivity increases, and the subordinate's relative fighting ability decreases.

The extended model (Reeve and Ratnieks 1993) assumed that breeders were symmetrically related to each other's offspring, as commonly occurs in "semisocial" associations, for example, the association of (potential) social insect queens of the same generation. Such associations can arise either when the queen disappears from a colony consisting of her daughters (i.e., in orphaned colonies) or when same-generation relatives (such as sibling nest foundresses in Polistes paper wasps) found nests together. In vertebrates, semisocial societies result when one individual cares for the brood of another individual of the same generation (e.g., the brood of a sibling).

We extend a simple version of the earlier model (Reeve and Ratnieks) by examining the consequences of queens having asymmetrical relatedness to each other's offspring, such as will occur when one potential breeder is the daughter of another breeder. The latter "matrifilial" associations often arise in eusocial insects. For example, in primitively eusocial insects such as Polistes paper wasps,
high-ranking workers that are descended from the founding queen exhibit queen-like behaviors and are capable of producing reproductive offspring (West-Eberhard 1969; Miyano 1986; review in Reeve 1991). In advanced eusocial insects, daughter queens are often allowed to remain in or are readopted into their natal colonies (secondary polygyny) (Stille et al. 1991; Rosengren et al. 1993). In vertebrates, matrilineal societies commonly result when offspring help their parents rear siblings before dispersing to reproduce on their own ("helpers-at-the-nest") (Emlen 1990). We shall present a theoretical argument that reproductive skews in matrilineal associations (asymmetrical relatednesses) will tend to be greater than those in semisocial associations (symmetrical relatednesses), even when breeders in each kind of association have the same relatedness to each other. We then present evidence supporting this prediction for both eusocial insects and social vertebrates.

THE MODEL

As in the previous models, we begin with the assumption that two breeders differ in dominance, relative dominance position being determined by relative fighting ability (perhaps assessed by relative size) or by conventional cues such as age or order of nest joining. The amount of reproduction yielded by a dominant to a subordinate should depend on (1) the subordinate’s prospects for successful nesting if it leaves the association (i.e., the severity of ecological constraints), (2) the productivity advantages of peaceful association, and (3) the relatedness between dominant and subordinate. (For simplicity, we ignore the modulation of the precise degree of skew by fighting ability and assume that relative fighting ability is important only in deciding who is dominant; later we will discuss the consequence of relaxing this assumption.) It is algebraically convenient to standardize variables 1 and 2 relative to the success of an already-established, independently founded nest and to express the relatednesses (3) as ratios of relatednesses to offspring (a procedure that allows for the possibility of asymmetrical relatednesses). Thus, four parameters enter into our two-breeder model: $x$ is the probability of successful nest foundation by a potential subordinate breeder times the proportional expected productivity of such a nest relative to that of an already-established singly founded nest (lower values of $x$ indicate harsher ecological constraints); $k$ is the ratio of the expected overall productivity of a joined nest to that of an established singly founded nest (assumed to be $> 1$); $r_{ds}$ is the relatedness of the dominant to the subordinate’s offspring, divided by the dominant’s relatedness to its own offspring; and $r_{sd}$ the relatedness of the subordinate to the dominant’s offspring, divided by the subordinate’s relatedness to its own offspring.

The proportion, $p$, of overall direct reproduction yielded to the subordinate in a stable association is that which gives the subordinate sufficient incentive to remain in the association (rather than leave and found a nest solitarily). This is the staying incentive discussed elsewhere (Reeve and Ratnieks 1993). We should point out that by "overall direct reproduction" we mean the total reproductive
output of individuals while they are members of the group. We do not consider
offspring production of individuals outside of the group (although inclusion of the
latter in skew calculations is useful for quantifying the overall degree of eusoci-
ality in animal societies; Sherman et al., in press). When individuals can repro-
duce outside of the group after dispersal, as in many social vertebrates, we
assume for simplicity that reproductive success outside of the group is not affected
by reproductive skews within groups.

Stable association results only when the subordinate is favored to join versus
nest solitarily and when the dominant is favored to accept versus reject the subor-
dinate. Thus, two decisions must be considered to arrive at the evolutionarily
stable skew (see also Reeve 1991). Decision i will be favored over decision j if

\[(P_i - P_j) + r(K_i - K_j) > 0,\]  

(1)

where \(r\) is the relevant coefficient of relatedness, \(P_i\) (or \(P_j\)) is the personal repro-
duction associated with strategy \(i\) (or \(j\)), and \(K_i\) (or \(K_j\)) is the other party’s repro-
duction if strategy \(i\) (or \(j\)) is performed (Hamilton 1964; Grafen 1984).

First we consider the question, Will the subordinate remain in the association
with no direct reproduction (i.e., for \(p = 0\))? The answer is yes if, from general
condition (1), \((0 - x) + r_{sd}(k - 1) > 0\), that is, when \(x < r_{sd}(k - 1)\). In this
situation, will the dominant accept the subordinate? Again applying condition (1),
but from the dominant’s point of view, we obtain the condition \((k - 1) + r_{ds}(0 - x) > 0\),
which yields \(x < (k - 1)/r_{ds}\). The latter must be true if the first
condition is true (because \([k - 1]/r_{ds} \geq r_{sd}(k - 1)]\), so that complete skew in a
stable association is expected when \(x < r_{sd}(k - 1)\). This is the same as the result
for breeders of symmetrical offspring relatedness \(r\); complete skew is expected
when \(x < r(k - 1)\).

Suppose now that \(x > r_{sd}(k - 1)\). The next question is, Does the dominant
yield the staying incentive? Here, the first problem is to quantify the staying
incentive, that is, to determine the minimum proportion of direct reproduction
necessary to induce the subordinate to stay. Following the approach cited else-
where (Reeve and Ratnieks 1993), we apply condition (1) to the subordinate’s
decision to stay (rather than leave) when the subordinate is yielded a fraction \(p\)
of the direct reproduction:

\[(pk - x) + r_{sd}[(1 - p)k - 1] > 0.\]  

(2)

Solving for \(p\) and converting the inequality into an equality, we obtain the staying
incentive \(p_s = (x - r_{sd}(k - 1))/k(1 - r_{sd})\) for \(r_{sd} < 1\).

What is the maximum staying incentive \(p_d\) allowed by the dominant? Proceed-
ing as before, we solve

\[[(1 - p_d)k - 1] + r_{ds}(p_d k - x) = 0,\]  

(3)

which yields, after simplification, \(p_d = (k - 1 - x r_{ds})/k(1 - r_{ds})\) for \(r_{ds} < 1\).

Stable association with a positive staying incentive for the subordinate thus
will result only when \(p_d > p_s\), that is, when

\[(k - 1 - x r_{ds})/(1 - r_{ds}) > [x - r_{sd}(k - 1)]/(1 - r_{sd}).\]  

(4)
Rearrangement of inequality (4) by cross multiplication and simplification yields the simple condition

$$x < k - 1.\quad (5)$$

When condition (5) holds, the staying incentive will equal $p_s$. This is the same as the condition for a staying incentive when breeders have symmetrical offspring relatedness (Reeve 1991; Reeve and Ratnieks 1993).

Although it may seem that symmetrical and asymmetrical breeder relatednesses lead to precisely the same skews (in both cases the degree of skew depends only on the quantity, $r_{sd}$), it must be remembered that condition (5) was derived only for the case in which $r_{sd}$ and $r_{ds}$ are both less than one. Now suppose $r_{sd} = 1$. Substituting this value into condition (2) yields only condition (5) again. In other words, in this case the subordinate queen is neutral about how much direct reproduction it receives; it will join (if $x < k - 1$) no matter what its share ($p$) of the direct reproduction. However, if in this case $r_{ds} < 1$, the dominant queen is not neutral about its share of the reproduction, and it is expected to completely monopolize the direct reproduction.

We can now compare the expected skews for matrifilial and semisocial associations. Consider a mother-daughter (matrifilial) association and a semisocial association consisting of two sisters (related by 0.50) and assume that, first, the daughter in the matrifilial association is the subordinate and, second, the sex ratio of reproductive offspring is 1:1 (we shall consider the effect of violation of the second assumption in haplodiploid species below). In both cases the two females are related to each other by the same amount. However, for the matrifilial association $r_{sd} = 0.50/0.50 = 1$ (assuming the mother mated with a single male) and $r_{ds} = 0.25/0.50 = 0.50$, whereas for the semisocial association both $r_{sd}$ and $r_{ds} = 0.25/0.50 = 0.50$. Thus, by the argument in the preceding paragraph, complete skew ($p_s = 0$) is expected in matrifilial associations when $x < k - 1$ (or else the subordinate is selected to breed independently). (The latter result is intimately related to the argument of Stubblefield and Charnov [1986] for the evolution of eusociality.) In contrast, in semisocial associations, complete skew is expected only when $x < 0.5(k - 1)$, which is a more restrictive condition than that for matrifilial associations. Furthermore, if $0.5(k - 1) < x < k - 1$, a fraction of the total direct reproduction will be offered to the subordinate by the dominant in semisocial associations, whereas the dominant will still completely monopolize reproduction in matrifilial associations. The overall theoretical prediction is that skews in simple matrifilial associations will tend to exceed skews of simple semisocial associations.

**Skews in Multiple-Breeder Matrifilial Associations**

Suppose the subordinate has some uncertainty about whether a controlling breeder is in fact its mother, as might occur in polygynous (multiple-queen) social insect colonies. In this case, the expected $r_{sd}$ is no longer equal to one, so the predicted skew may be partial, that is, equal to the staying incentive. Even in this case, however, asymmetrical relatedness has an effect (although diluted by the degree of subordinate uncertainty over maternity): The staying incentive de-
creases with increasing expected $r_{sd}$, and the presence of the mother among the dominant breeders will always cause the latter value to be higher than if the controlling queens always consisted only of other kin (e.g., siblings or aunts). Thus, presence of the mother in a group of dominant breeders will still tend to enhance the skew. (Female breeder mating frequency will have little effect on this prediction: Polyandry by females will reduce mean relatedness of a female to the mother’s offspring but also to the offspring of other non descendant relatives, such as aunts, and to the offspring of same-generation relatives, such that the relatedness asymmetry is preserved.) In sum, a generally greater reproductive skew is expected in matrilial than in semisocial societies (fig. 1), regardless of whether the matrilial societies consist of one or multiple queens.

*Skews in Matrilial Associations When Daughters Can Produce Only Males*

As a consequence of the haplodiploid sex-determination system, only mated females can produce female offspring in the Hymenoptera. A hymenopteran queen can sometimes be replaced by an unmated worker (Chandrashekara and Gadagkar 1991; Reeve 1991). In this case asymmetrical relatedness will tend to enhance skew even if the subordinate is only able to produce males. If the dominant queen (mother) produces reproductive offspring at an even sex ratio, an unfertilized subordinate is, on the average, still more highly related to its siblings than to the male offspring of unfertilized siblings. Only if the mother produces a sufficiently male-biased sex ratio can a situation arise in which an unfertilized
worker is more closely related to the offspring of its unfertilized siblings than to the offspring of its mother, which would result in a greater skew in the semisocial than in the corresponding matrilineal association. As an example of the latter situation, if a singly mated queen produces only males, a worker will be more highly related to nephews \( (r = 3/8) \) than to brothers \( (r = 1/4) \), and thus the higher skew would be predicted for semisocial sister associations. However, the conditions for such a skew reversal to occur are somewhat restrictive: A low queen mating frequency must be coupled to a highly male-biased sex ratio of the mother’s offspring, or else unmated daughters will have a higher expected relatedness to the mother’s offspring than to each other’s offspring. There are theoretical reasons for expecting just the reverse association, that is, that relatively low queen mating frequency will be associated with a female-biased colony sex ratio (Boomsma and Grafen 1990).

**Influences of Independent Breeding Constraints and Fighting Ability on Reproductive Skew**

The optimal skew models also predict that constraints on solitary reproduction and relative fighting abilities of females should modulate the reproductive skew (Reeve 1991; Reeve and Ratnieks 1993). In particular, lesser fighting ability of the subordinate female or lower probability that the latter can successfully reproduce solitarily (i.e., low \( x \) in fig. 1) should lead to higher proportionate reproduction by the dominant female (Reeve and Ratnieks 1993). Both of these factors should tend to reinforce the prediction from consideration of relatedness symmetry alone that skews should be higher in matrilineal than in semisocial associations. In particular, social insect workers typically are smaller than their mother queen, which suggests that they possess lower fighting ability, and their prospects for successful independent nesting appear low (especially for small daughter workers that emerge late in the colony cycle in temperate species). Thus it seems reasonable to make the general prediction that matrilineal societies will exhibit higher skew than semisocial societies, particularly in (but not restricted to) cases in which subordinates of matrilineal colonies are smaller than their queen and have more limited options for personal reproduction away from the nest.

The contributions of relatedness asymmetry, solitary breeding constraints, and fighting abilities to the different skews of matrilineal and semisocial societies are not easily disentangled, particularly in the social insects. However, the skew models predict that relatedness asymmetry will lead to higher skew in matrilineal associations even when a subordinate is similar in size and physiology (and, thus, presumably in ability both to fight and to nest separately) to the dominant. This would seem most likely to be true for social vertebrates in which subordinates are mature adults (see below). Even in the social insects, workers are sometimes as large as, or even larger than, their queen, particularly in “primitively eusocial” species (e.g., see review in Reeve 1991 for polistine wasps). Decisive evidence of the role of relatedness asymmetry in the evolution of skew requires analysis of the reproductive skews in the above cases. First, however, it is necessary to ascertain whether reproductive skews do in fact differ between matrilineal and semisocial associations.
EVIDENCE OF REPRODUCTIVE SKEWS IN MATRIFILIAL VERSUS SEMISOCIAL ASSOCIATIONS

Social Insects

Evidence exists that the reproductive division of labor is more equitable in semisocial than in matrifilial associations in social insects. In table 1, we present quantitative data on reproductive skew in semisocial and matrifilial associations of the same species for various eusocial Hymenoptera. We restricted our attention to associations in which dominance is known to occur or at least for which group size is not too large to preclude manipulation of reproduction by dominant individual(s). In very large associations (≥10^3 individuals), such as worker groups in honey bees and many ant species, dominance is expected to break down and factors other than behavioral dominance should regulate the reproductive skew (Keller and Nonacs 1993; Reeve and Ratnieks 1993). The data generally corroborate the theoretical prediction that skew tends to be lower in semisocial associations. In 13 of 17 cases (76%), matrifilial skew exceeded semisocial skew, whereas in only one case (6%) semisocial skew exceeded matrifilial skew (mean values were used when skew values were available from more than one study) (sign test, P < .01).

Particularly interesting is evidence suggesting that "functional monogyny" (or, in our terms, maximum reproductive skew) may be characteristic of secondarily polygynous ant colonies consisting of a mother queen and subordinate daughter queens (Heinze and Smith 1990). Our model predicts that functional monogyny should often be associated with associations of mother and daughter queens (or at least with high between-queen relatednesses). Indeed, young queens have been shown to be reaccepted in their mother nest in functionally monogynous ants of the genus Leptothorax (Heinze and Buschinger 1988). Furthermore, it has recently been discovered that the mean relatedness of queens in Leptothorax gredleri is 0.34 and may be as high as 0.50 (J. Heinze, personal communication), both of which are relatively high values of queen-queen relatedness for associations of ant queens (Hölldobler and Wilson 1990; Rosengren et al. 1993). Modern genetic methods (e.g., DNA fingerprinting, microsatellite analysis) now make many more such tests feasible.

Social Vertebrates

In table 2 are presented available data on skew in matrifilial versus semisocial societies of 20 vertebrate (bird and mammal) species. We restrict our attention to cooperating females because data on male paternity and hence male reproductive skew are available for few species. The matrifilial associations are associations in which a female helper assists its parents in raising siblings; the semisocial associations are groups of cooperating females likely to be siblings or at least of the same generation.

The data strongly indicate that maximum skew (i.e., complete reproductive monopoly) is much more likely to occur in matrifilial than in semisocial associations, the latter frequently being characterized by skew less than one (i.e., multiple maternity of offspring within a social group). Moreover, several species (acorn woodpeckers, arabian babblers, groove-billed anis, Mexican jays, and pukekos)
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<th>Matrilineal Colonies</th>
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<td>Less spp.</td>
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<td>Dwarf mongooses (Helogale parvula; 12)*</td>
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<td>Banded mongooses (M. mungo; 12)*</td>
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<td>Spotted hyenas (Crocuta crocuta; 20)</td>
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</table>


* Includes groups exhibiting more than one combination of social system and reproductive skew.

appear to exhibit both conditions simultaneously. For example, in acorn woodpecker and pukéko societies, helping daughters of a breeding pair themselves are nonbreeders, whereas cooperating sisters usually share in the production of offspring (Craig and Jamieson 1990; Koenig and Stacey 1990). Some of the apparent exceptions to the predictions (e.g., skews less than one in matrilinal associations of banded mongooses) are merely possibilities that cannot be ruled out by the data, owing to uncertainties in genetic relatedness between specific pairs of individuals.
CONCLUSIONS

A survey of reproductive partitioning within invertebrate and vertebrate societies strongly supports the prediction from optimal skew theory that reproductive skews should be higher in matrilineal (asymmetrical relatedness) than in semisocial (symmetrical relatedness) animal societies. In many cases (especially in the social insects), the higher skews in matrilineal associations may result from greater ecological constraints on subordinate reproduction or from the greater disparity of fighting abilities of dominants and subordinates in matrilineal versus semisocial systems (as also predicted optimal skew theory; see above). However, the relatedness asymmetry in matrilineal associations accounts for the reproductive monopoly in cases in which the latter two factors are likely unimportant, such as for vertebrates (e.g., bee eaters) in which mothers and daughters in matrilineal groups are similarly sized, mature adults probably of similar fighting ability and similarly capable of breeding separately.

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LITERATURE CITED


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