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

HUDSON K. REEVE[1] AND LAURENT KELLER[2]

[1]Section of Neurobiology and Behavior, Seeley G. Mudd Hall, Cornell University, Ithaca, New York 14853; [2]Zoologisches Institut, Bern University, Ethologische Station Hasli, Wohlenstrasse 50a, 3032 Hinterkappelen, Switzerland, and Institut de Zoologie et d'Ecologie Animale, University of Lausanne, Bâtiment de Biologie, 1015 Lausanne, Switzerland

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 matrifilial (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 (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 matrifilial 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 matrifilial 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 $(N_b v + N_n)/(N_b + N_n)$, 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., $s^2 = [\Sigma(p_i - 1/N_b)^2]/[N_b - 1]$, where p_i is the proportion of all offspring produced by the ith 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, matrifilial 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 matrifilial 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 eusociality in animal societies; Sherman et al., in press). When individuals can reproduce 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 subordinate. 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

$$(P_i - P_j) + r(K_i - K_j) > 0 , \tag{1}$$

where r is the relevant coefficient of relatedness, P_i (or P_j) is the personal reproduction associated with strategy i (or j), and K_i (or K_j) is the other party's reproduction if strategy i (or j) is performed (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 elsewhere (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:

$$(pk - x) + r_{sd}[(1 - p)k - 1] > 0 . \tag{2}$$

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? Proceeding as before, we solve

$$[(1 - p_d)k - 1] + r_{ds}(p_d k - x) = 0 , \tag{3}$$

which yields, after simplification, $p_d = (k - 1 - xr_{ds})/k(1 - r_{ds})$ 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

$$(k - 1 - xr_{ds})/(1 - r_{ds}) > [x - r_{sd}(k - 1)]/(1 - r_{sd}) . \tag{4}$$

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

$$x < k - 1. \tag{5}$$

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-

SEMISOCIAL SOCIETY
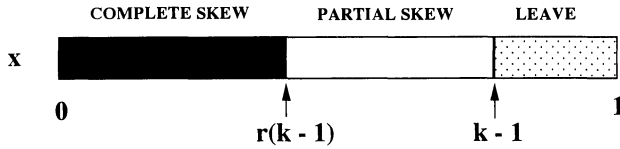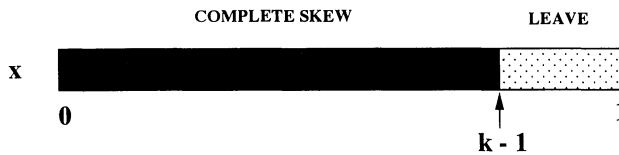

MATRIFILIAL SOCIETY

Fig. 1.—Reproductive skews in semisocial (same-generation, e.g., sibling) associations
(*top*) and mother-daughter associations (*bottom*), as a function of the ecological constraint
parameter, x, the group productivity parameter, k (see text), and the relatedness between
queens, r. If $x > k - 1$, no association is formed because the subordinate leaves to reproduce
independently.

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 nondescendant rela-
tives, 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 matrifilial than in semisocial societies (fig. 1), regardless of
whether the matrifilial societies consist of one or multiple queens.

Skews in Matrifilial 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 (Chandrasherkara 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 domi-
nant 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 matrifilial 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 matrifilial 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 matrifilial societies will exhibit higher skews than semisocial societies, particularly in (but not restricted to) cases in which subordinates of matrifilial 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 matrifilial and semisocial societies are not easily disentangled, particularly in the social insects. However, the skew models predict that relatedness asymmetry will lead to higher skews in matrifilial 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 matrifilial 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 skews within 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 ($\geq 10^3$ 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 skews tend 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 skews 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 skews 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 skews 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)

TABLE 1

COMPARISONS OF REPRODUCTIVE SKEWS IN SEMISOCIAL (SYMMETRICALLY RELATED) AND
MATRIFILIAL (ASYMMETRICALLY RELATED) QUEEN ASSOCIATIONS

	SEMISOCIAL COLONIES		MATRIFILIAL COLONIES	
SPECIES	Skew (N)	Source	Skew (N)	Source
Ants:				
Leptothorax (s. str.) sp. A	1.00 (3)[e,r*]	1	1.00 (5)[e]	1
Bees:				
Augochlorella striata	< 1.00 (12)[g,r]	2	1.00 (12)[g]	2
Bombus terrestris	.05 (1)[e,n]	3	1.00 (1)[e]	3
Bombus spp.	Less[o,n]	4	More[o]	4
Lasioglossum (*Dialictus*) spp.	≤ 1.00[o,e]	5	1.00[o,e]	5
Xylocopa pubescens	1.00 (2)[e,n]	6	1.00 (6)[e]	6
Wasps:				
Polistes chinensis antennalis	.09 (1)[e,n]	7	.40 (2)[e]	8
Polistes dominulus	< 1.0 (3)[o,n]	9	1.0 (17)[o]	9
	< 1.0 (7)[e,n*]	10		
Polistes exclamans	1.00 (4)[o,n*]	11	1.00 (7)[o,e]	11, 12
	1.00 (5)[e,n*]	13		
Polistes fuscatus	1.00 (5)[o,n*]	14	1.00 (8)[o]	14
	.70 (4)[e,n*]	15	1.00 (4)[g]	16
	.53 (6)[e,n*]	15		
Polistes jadwigae	< 1.00 (2)[e,n]	17	1.00 (1)[e]	17
	< 1.00 (1)[e,n*]	18		
	.44 (1)[e,n*]	19		
Polistes metricus	.42 (7)[g,n*]	20	.98 (6)[g]	20
	1.00 (8)[e,n*]	21		
	.02 (3)[e,n*]	21		
	.90 (13)[e,n]	20		
Polistes snelleni	.87 (3)[e,n]	22	1.00 (5)[e]	22
	< 1.00 (2)[e,r]	23		
Ropalidia fasciata	.61 (4)[o,n]	24	.71 (10)[o]	24
Ropalidia gregaria gregaria	.44 (1)[o,n]	24	.88 (3)[o]	24
Ropalidia revolutionalis	1.00 (7)[o,n]	24	.66 (9)[o]	24
Ropalidia sp. nr. *variegata*	.42 (2)[o,n]	24	1.00 (4)[o]	24

NOTE.—First superscripts o, e, and g refer to assessment of reproductive division of labor by ovarian or egg development, egg-laying, or genetic analyses, respectively. Second superscripts n and r indicate that semisocial associations were formed naturally or by experimental removal of the presumed mother queen. Asterisks indicate semisocial associations of morphologically similar queens; other semisocial associations are queenless worker colonies. Number of colonies is given as N. Numbered references are 1, Heinze and Smith 1990; 2, U. G. Mueller, personal communication; 3, van Honk et al. 1981; Owen and Plowright 1982; 4, Sakagami 1976; 5, review in Michener 1974, Eickwort 1986; 6, van der Blom and Velthius 1988; 7, Miyano 1986 (maximum possible skew); 8, Miyano 1980; 9, Turillazzi 1980; 10, Gervet 1964; 11, Strassmann 1981; 12, Strassmann 1981, Strassmann and Meyer 1983, Lester and Selander 1981; 13, Hughes and Strassmann 1988 (top: two-queen associations; bottom: three-queen associations); 14, Page et al. 1989; 15, Noonan 1981 (top: two-queen associations; bottom: maximum possible skew, three- to six-queen associations); 16, Metcalf 1980; 17, Miyano 1991; 18, Kasuya 1981; 19, Tsuchida and Itô 1991; 20, Metcalf and Whitt 1977; 21, Gamboa et al. 1978 (top value: two-foundress associations; bottom value: three-foundress associations); 22, Suzuki 1987; 23, Suzuki 1985; 24, Itô, 1993 (skews calculated on assumption that "egg-layers" equally divided reproduction).

TABLE 2

COMPARISONS OF REPRODUCTIVE SKEWS AMONG FEMALES IN MATRIFILIAL AND
SEMISOCIAL VERTEBRATE SOCIETES

Skew = 1.0	Skew < 1.0
Matrifilial:	
Acorn woodpeckers (*Melanerpes formiciv-orous;* 1)*	Banded mongooses (*Mungos mungo;* 12)*
Arabian babblers (*Turdoides squamiceps;* 2)*	
Florida scrub jays (*Aphelocoma coerulescens;* 3)	
Green wood hoopoes (*Phoeniculus purpureus;* 4)	
Hoatzins (*Opisthocomus hoazin;* 5)	
Mexican jays (*Aphelocoma ultramarina;* 6)*	
Pukeko (*Porphyrio porphyrio;* 7)*	
Splendid fairy wrens (*Malurus splendens;* 8)	
Stripe-backed wrens (*Campylorhynchus nuchalis;* 9)	
White-fronted bee-eaters (*Merops bullockoides;* 10)	
Groove-billed anis (*Crotophaga sulcirostris;* 19)*	
Damaraland mole-rat (*Cryptomys damarensis;* 11)	
Dwarf mongooses (*Helogale parvula;* 12)*	
Golden jackal (*Canis aureus;* 13)	
Marmosets (*Saguinus* spp.; 14)	
Naked mole-rat (*Heterocephalus glaber;* 15)	
Silver-backed jackal (*Canis mesolmelas;* 13)	
Tamarins (*Callithrix* spp.; 16)	
Wild dogs (*Lycaon pictu;* 17)	
Semisocial:	
Arabian babblers (*T. squamiceps;* 2)*	Acorn woodpeckers (*M. formicivorous;* 1)*
Mexican jays (*A. ultramarina;* 6)*	Arabian babblers (*T. squamiceps;* 2)*
Dwarf mongooses (*H. parvula;* 12)*	Galápagos mockingbirds (*Nesomimus parvulus;* 18)
	Groove-billed anis (*C. sulcirostris;* 19)*
	Mexican jays (*A. ultramarina;* 6)*
	Pukeko (*P. porphyrio;* 7)*
	Banded mongooses (*M. mungo;* 12)*
	Spotted hyenas (*Crocuta crocuta;* 20)

SOURCES.—1, Koenig and Mumme 1987, Koenig and Stacey 1990; 2, Zahavi 1990; 3, Woolfenden and Fitzpatrick 1984; 4, Ligon and Ligon 1990; 5, Strahl and Schmitz 1990; 6, Brown and Brown 1990; 7, Craig and Jamieson 1990; 8, Rowley and Russell 1990; 9, Rabenold 1990; 10, Emlen 1990; 11, Bennett and Jarvis 1988; 12, Rood 1986; 13, Moehlman 1986; 14, Snowdon and Soini 1988; 15, Sherman et al. 1991; 16, Stevenson and Rylands 1988; 17, Frame et al. 1979, Malcolm and Marten 1982; 18, Curry and Grant 1990; 19, Vehrencamp et al. 1988; 20, Frank 1986, Koford et al. 1990.
  * Includes groups exhibiting more than one combination of social system and reproductive skew.

appear to exhibit both conditions simultaneously. For example, in acorn wood-pecker and pukeko 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 matrifilial 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 matrifilial (asymmetrical relatedness) than in semisocial (symmetrical relatedness) animal societies. In many cases (especially in the social insects), the higher skews in matrifilial associations may result from greater ecological constraints on subordinate reproduction or from the greater disparity of fighting abilities of dominants and subordinates in matrifilial versus semisocial systems (as also predicted optimal skew theory; see above). However, the relatedness asymmetry in matrifilial 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 matrifilial groups are similarly sized, mature adults probably of similar fighting ability and similarly capable of breeding separately.

LITERATURE CITED

Bennett, N. C., and J. U. M. Jarvis. 1988. The social structure and reproductive biology of colonies of the mole-rat *Cryptomys damarensis* (Rodentia, Bathyergidae). Journal of Mammology 69:293–302.

Boomsma, J. J., and A. Grafen. 1990. Intraspecific variation in ant sex ratios and the Trivers-Hare hypothesis. Evolution 44:1026–1034.

Brown, J. L., and E. R. Brown. 1990. Mexican jays: uncooperative breeding. Pages 267–288 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Chandrasherkara, K., and R. Gadagkar. 1991. Unmated queens in the primitively eusocial wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). Insectes Sociaux 38:213–216.

Craig, J. L., and I. G. Jamieson. 1990. Pukeko: different approaches and some different answers. Pages 385–412 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Curry, R. L., and P. R. Grant. 1990. Galápagos mockingbirds: territorial cooperative breeding in a climatically variable environment. Pages 289–332 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Eickwort, G. C. 1986. First steps into eusociality: the sweat bee *Dialictus lineatulus*. Florida Entomologist 69:743–744.

Emlen, S. T. 1990. White-fronted bee-eaters: helping in a colonially nesting species. Pages 487–526 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Frame, L. H., J. R. Malcolm, G. W. Frame, and H. van Lawick. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania, 1967–1978. Zeitschrift für Tierpsychologie 50:225–249.

Frank, L. G. 1986. Social organization of the spotted hyena *Crocuta crocuta*. II. Dominance and reproduction. Animal Behaviour 34:1510–1527.

Gamboa, G. J., B. D. Heacock, and S. L. Wiltjer. 1978. Division of labor and subordinate longevity in foundress associations of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). Journal of the Kansas Entomological Society 51:343–352.

Gervet, J. 1964. La ponte et sa régulation dans la société polygyne de *Polistes gallicus* L. (Hyménoptère Vespidé). Annales des Sciences Naturelles Zoologie Biologie Animale (Sér. 12) 6: 601–778.

Grafen, A. 1984. Natural selection, kin selection, and group selection. Pages 62–89 *in* J. R. Krebs and N. B. Davies, eds. Behavioral ecology: an evolutionary approach. 2d ed. Sinauer, Sunderland, Mass.

Hamilton, W. D. 1964. The genetical evolution of social behavior. I, II. Journal of Theoretical Biology 7:1–52.

Heinze, J., and A. Buschinger. 1988. Polygyny and functional monogyny in *Leptothorax* ants (Hymenoptera: Formicidae). Psyche 95:309–325.

Heinze, J., and T. A. Smith. 1990. Dominance and fertility in a functionally monogynous ant. Behavioral Ecology and Sociobiology 27:1–10.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, Mass.

Hughes, C. R., and J. E. Strassmann. 1988. Foundress mortality after worker emergence in social wasps (*Polistes*). Ethology 79:265–281.

Itô, Y. 1993. The evolution of polygyny in primitively eusocial polistine wasps with special reference to the genus *Ropalidia*. Pages 171–187 *in* L. Keller, ed. Queen number and sociality in insects. Oxford University Press, Oxford.

Kasuya, E. 1981. Polygyny in the Japanese paper wasp, *Polistes jadwigae* Dalla Torre (Hymenoptera, Vespidae). Kontyû 49:306–313.

Keller, L., and P. Nonacs. 1993. The role of queen pheromones in colonies of social insects: queen control or queen signal? Animal Behaviour 45:787–794.

Keller, L., and E. L. Vargo. 1993. Reproductive structure and reproductive roles in colonies of eusocial insects. Pages 16–44 *in* L. Keller, ed. Queen number and sociality in insects. Oxford University Press, Oxford.

Koenig, W. D., and R. L. Mumme. 1987. Population ecology of the cooperatively breeding acorn woodpecker. Princeton University Press, Princeton, N.J.

Koenig, W. D., and P. B. Stacey. 1990. Acorn woodpeckers: group-living and food storage under contrasting ecological conditions. Pages 413–454 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Koford, R. R., B. S. Bowen, and S. L. Vehrencamp. 1990. Groove-billed anis: joint-nesting in a tropical cuckoo. Pages 333–356 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Lester, L. J., and R. K. Selander. 1981. Genetic relatedness and the social organization of *Polistes* colonies. American Naturalist 117:147–166.

Ligon, J. D., and S. H. Ligon. 1990. Green woodhoopoes: life history traits and sociality. Pages 31–66 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge, Cambridge University Press.

Malcolm, J. R., and K. Marten. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). Behavioral Ecology and Sociobiology 10:1–13.

Metcalf, R. A. 1980. Sex ratios, parent-offspring conflict, and local competition for mates in the social wasps *Polistes metricus* and *Polistes variatus*. American Naturalist 116:642–654.

Metcalf, R. A., and G. S. Whitt. 1977. Intra-nest relatedness in the social wasp *Polistes metricus:* a genetic analysis. Behavioral Ecology and Sociobiology 2:339–351.

Michener, C. D. 1974. The social behavior of bees: a comparative study. Harvard University Press, Cambridge, Mass.

Miyano, S. 1980. Life tables of colonies and workers in a paper wasp, *Polistes chinensis antennalis* in central Japan (Hymenoptera: Vespidae). Researches on Population Ecology 22:69–88.

———. 1986. Colony development, worker behavior and male production in orphan colonies of a Japanese paper wasp, *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). Researches on Population Ecology 28:347–361.

————. 1991. Worker reproduction and related behavior in orphan colonies of a Japanese paper wasp, *Polistes jadwigae* (Hymenoptera, Vespidae). Journal of Ethology 9:135–146.

Moehlman, P. D. 1986. Pages 64–86 *in* D. I. Rubenstein and R. W. Wrangham, eds. Ecological aspects of social evolution. Princeton University Press, Princeton, N.J.

Noonan, K. M. 1981. Individual strategies of inclusive-fitness-maximizing in *Polistes fuscatus* foundresses. Pages 18–44 *in* R. D. Alexander and D. W. Tinkle, eds. Natural selection and social behavior: recent research and new theory. Chiron, New York.

Owen, R. E., and R. C. Plowright. 1982. Worker-queen conflict and male parentage in bumble bees. Behavioral Ecology and Sociobiology 11:91–99.

Page, R. E., Robinson, G. E., and R. A. Metcalf. 1989. Satellite nests, early males, and plasticity of reproductive behavior in a paper wasp. American Naturalist 134:731–748.

Rabenold, K. N. 1990. *Campylorhynchus* wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. Pages 157–196 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Reeve, H. K. 1991. *Polistes*. Pages 99–148 *in* K. Ross and R. Matthews, eds. The social biology of wasps. Cornell University Press, Ithaca, N.Y.

Reeve, H. K., and P. Nonacs. 1992. Social contracts in wasp societies. Nature (London) 359:823–825.

Reeve, H. K., and F. L. W. Ratnieks. 1993. Queen-queen conflict in polygynous societies: mutual tolerance and reproductive skew. Pages 45–85 *in* L. Keller, ed. Queen number and sociality in insects. Oxford University Press, Oxford.

Rood, J. P. 1986. Ecology and social evolution in the mongooses. Pages 131–152 *in* D. I. Rubenstein and R. W. Wrangham, eds. Ecological aspects of social evolution. Princeton University Press, Princeton, N.J.

Rosengren R., L. Sundstöm, and W. Fortelius. 1993. Monogyny and polygyny in *Formica* ants: the result of alternative dispersal tactics. Pages 308–333 *in* L. Keller, ed. Queen number and sociality in insects. Oxford University Press, Oxford.

Rowley, I. C. R., and E. Russell. 1990. Splendid fairy-wrens: demonstrating the importance of longevity. Pages 1–30 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Sakagami, S. F. 1976. Specific differences in the bionomic characters of bumblebees: a comparative review. Journal of Factual Sciences at Hokkaido University, Series VI, Zoology 20:390–445.

Sherman, P. W., J. U. M. Jarvis, and R. D. Alexander, eds. 1991. The biology of the naked mole-rat. Princeton University Press, Princeton, N.J.

Sherman, P. W., E. A. Lacey, H. K. Reeve, and L. Keller. In press. The eusociality continuum. Behavioral Ecology.

Snowdon, C. T., and P. Soini. 1988. The tamarins, genus *Saguinus*. Pages 223–298 *in* R. A. Mittermeier, A. F. Coimbra-Filho, and G. A. B. da Fonseca, eds. Ecology and behavior of Neotropical primates. Vol. 2. World Wildlife Fund, Washington, D.C.

Stevenson, M. F., and A. B. Rylands. 1988. The marmosets, genus *Callithrix*. Pages 131–222 *in* R. A. Mittermeier, A. F. Coimbra-Filho, and G. A. B. da Fonseca, eds. Ecology and behavior of Neotropical primates. Vol. 2. World Wildlife Fund, Washington, D.C.

Stille, M., B. Stille, and P. Douwes. 1991. Polygyny, relatedness and nest founding in the polygynous myrmicine ant *Leptothorax acervorum* (Hymenoptera; Formicidae). Behavioral Ecology and Sociobiology 28:91–96.

Strahl, S. D., and A. Schmitz. 1990. Hoatzins: cooperative breeding in a folivorous Neotropical bird. Pages 131–156 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Strassmann, J. E. 1981. Kin selection and satellite nests in *Polistes exclamans*. Pages 45–58 *in* R. D. Alexander and D. W. Tinkle, eds. Natural selection and social behavior: recent research and new theory. Chiron, New York.

Strassmann, J. E., and D. C. Meyer. 1983. Gerontocracy in the social wasp *Polistes exclamans*. Animal Behaviour 31:431–438.

Stubblefield, J. W., and E. L. Charnov 1986. Some conceptual issues in the origin of eusociality. Heredity 57:181–187.

Suzuki, T. 1985. Mating and laying of female-producing eggs by orphaned workers of a paper wasp, *Polistes snelleni* (Hymenoptera: Vespidae). Annals of the Entomological Society of America 78:736–739.

———. 1987. Egg-producers in the colonies of a polistine wasp, *Polistes snelleni* (Hymenoptera: Vespidae), in central Japan. Ecological Research 2:185–189.

Tsuchida, K., and Y. Itô. 1991. Negative correlation between dominance and frequencies of oviposition and oophagy in a foundress association of the Japanese paper wasp, *Polistes jadwigae* Dalla Torre (Hymenoptera: Vespidae). Applied Entomology and Zoology 26:443–448.

Turillazzi, S. 1980. Seasonal variation in the size and anatomy of *Polistes gallicus* (L.) (Hymenoptera: Vespidae). Monitore Zoologica Italiano, N.S., 14:63-75.

van der Blom, J., and H. H. W. Velthuis. 1988. Social behaviour of the carpenter bee *Xylocopa pubescens* (Spinola). Ethology 79:281–294.

van Honk, C. P., P. F. Röseler, H. H. W. Velthuis, and J. C. Hoogeven. 1981. Factors influencing the egg-laying of workers in a captive *Bombus terrestris* colony. Behavioral Ecology and Sociobiology 9:9–14.

Vehrencamp, S. L. 1983*a*. A model for the evolution of despotic versus egalitarian societies. Animal Behaviour 31:667–682.

———. 1983*b*. Optimal degree of skew in cooperative societies. American Zoologist 23:327–335.

West-Eberhard, M. J. 1969. The social biology of polistine wasps. Miscellaneous Publications of the Museum of Zoology, University of Michigan 140:1–101.

Wilson, E. O. 1971. The insect societies. Harvard University Press, Cambridge.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida scrub-jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, N.J.

Zahavi, A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. Pages 103–130 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.