Synergism between sib-rearing and sex ratio in Hymenoptera

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Summary. In many bees and wasps, solitary females produce offspring without help from other females. The transition from lone mothers producing offspring to situations in which females often help to rear siblings is an important step in the origins of complex sociality and nonreproductive castes. Recent work on Hymenoptera has stressed the role of sex ratio variation in this transition; when a mother's brood is more female biased than average, older daughters are favored to help rear their younger siblings because they are more closely related to sisters than to their own offspring. Here the direction of causality is from biased sex ratios, which arise by some extrinsic mechanism, to the origins of sib-rearing (eusociality). We present a model in which there is a synergism between sib-rearing and female-biased sex ratios, which may either complement the sex ratio variation idea by increasing the rate at which helping spreads or be an alternative hypothesis about the origins of eusociality. The synergism in our model depends on three conditions. 1) Daughters that help cause more food to be provisioned per offspring, which in turn causes larger offspring. 2) Females gain more than males by being large, which favors mothers with helpers to produce a higher proportion of daughters. 3) A helper's inclusive fitness rises as her mother's brood becomes increasingly female biased because a female helper is more closely related to her sisters than to her brothers. A female helper may also be more closely related to her sisters than to her own offspring, but this particular sibling-offspring relatedness asymmetry is not required by the synergism model. These three conditions create a synergism which favors a rapid transition from solitary (subsocial) to eusocial. De-mographic and ecological factors that facilitate the evolution of eusociality reduce the stringency of the relatedness asymmetry condition (3) required by our idea. The synergism model therefore complements factors other than relatedness that may have been important during the evolution of eusociality.

Introduction

Hymenopteran females often provide food for larvae. These larvae may be offspring, siblings or more distant kin. The evolutionary transition from females raising only offspring to sometimes rearing siblings is an important step in the origins of complex sociality and nonreproductive castes.

Several ideas have been proposed to explain the many independent origins of sib-rearing and the subsequent evolution of complex social groups (e.g., Andersson 1984; Brockmann 1984; Brown 1987). One class of argument focuses on the haplodiploid Hymenoptera, a group with several independent origins of sib-rearing and the most advanced forms of sociality. In these arguments relatedness asymmetries play a key role. Hymenopteran females are more closely related to their sisters than to their brothers and may be more closely related to their sisters than to their own sons or daughters (Hamilton 1964). Broods with relatively female-biased sex ratios are particularly conducive for sib-rearing because female helpers will be raising a high proportion of closely related sisters (Hamilton 1964, 1972; Trivers and Hare 1976). Predictable patterns of sex ratio variation may therefore facilitate the origin of sib-rearing (Iwasa 1981; Seger 1983; Grafen 1986; Godfray

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and Grafen 1988). In this paper we use the phrase 'sex ratio' to refer to the relative allocation of resources to males and females rather than the relative number of male and female individuals.

A second class of argument about complex sociality stresses that sib-rearing has evolved a number of times in diploid organisms, including termites and several birds and mammals. Demographic and ecological factors that are independent of relatedness asymmetries must be involved in these cases and probably have a strong influence on the Hymenoptera as well (e.g., Hamilton 1972; Lin and Michener 1972; Alexander 1974; Wilson 1975; West-Eberhard 1978). Demographic-ecological factors include the probability of nest success as a function of colony size and the availability of nest sites for establishing a new colony (for recent reviews, see Andersson 1984; Brockmann 1984; Brown 1987).

We focus on the first class of explanations for Hymenoptera – explanations that depend on the relatedness asymmetries of haplodiploid organisms. In particular, our model describes a mechanism by which there is a synergism between females that rear their sibs and mothers that produce a sex ratio more female biased than the population average. This synergism may partly explain the prevalence of sib-rearing among the Hymenoptera.

Although we focus on relatedness, our model does not exclude the importance of demographic aspects of social evolution. For example, if demographic variables have influenced the origins of sib-rearing in some groups, then our idea may explain the frequency and rapidity of transitions to more advanced forms of sociality. An interaction between demography and relatedness factors reduces the stringency of the relatedness condition of our model and therefore increases the plausibility of our idea. We stress this in the introduction in order to avoid the common tendency for approaches to be classified as either a relatedness model or an ecological-demographic model.

In the present paper we describe the model verbally and summarize the available evidence from bees and wasps. In a future paper a quantitative theory will be presented for the joint evolution of sib-rearing and sex allocation.

Brockmann and Grafen (in press) have independently developed an analogous idea for the evolution of male nest-guarding in certain wasp species. They provide evidence from *Trypoxylon politum* that guarding causes a bias in sex ratio towards daughters, and, because of the haplodiploid genetic system of wasps, a higher proportion of daughters enhances the fitness of a male guard.

Conditions for the synergism model

Consider a bee or wasp species in which the first daughters that a mother produces become adult while the mother is still active and laying eggs. The newly adult daughters may stay near the safety of their mother's nest while they feed and continue to mature, or they may go off by themselves. If they stay, they may help provision the offspring that their mother continues to produce or help guard the nest.

The synergism model depends on three conditions. 1) Mothers with more than an average amount of help tend to have larger than average offspring. 2) Large offspring are typically female. 3) Females are more closely related to their sisters than to their brothers.

When daughters in some broods help more than average, their mothers are favored to produce a greater proportion of female offspring (1 and 2). The resulting female bias favors an increase in the amount of helping by daughters because of relatedness asymmetries (3). Alternatively, if initially some broods have a higher proportion of females, then females from these broods are favored to invest more energy in sib-rearing. The increase in help favors the maintenance of an excess proportion of female progeny. *A synergistic interaction favors the maintenance of a greater than average proportion of female offspring in broods associated with a greater than average amount of sib-rearing.* The model does not necessarily predict that the population sex ratio changes as helping spreads, nor that average size of offspring changes, since the synergism is between excess help and an excess proportion of female progeny within broods.

These three simple conditions lead to a synergism between sib-rearing and female-biased sex ratios in broods with extra help. How realistic are these conditions? We summarize the available data, focusing mainly on solitary and primitively eusocial species because the model is about the origins and subsequent spread of sib-rearing within populations rather than the maintenance of eusociality in highly evolved societies.

1. More food per offspring is provided when daughters help, and this extra food leads to larger or more vigorous offspring

There are at least four plausible ways in which this might happen. First, mothers may tend to oviposit and permanently close a cell after a fixed foraging period. For example, the number of cells

per day that a colony can produce may depend on the timing and number of eggs that the queen matures per day. Provisions per cell would then be strongly influenced by the number of females that cooperate to provision the cells during the limited time available before oviposition and final cell closure. Batra (1968) reported that in several species of halictine bees eggs are usually laid in the late afternoon or early evening. Moreover, when food abundance declines, completed cells of halictine bees have fewer provisions (Batra 1966) which suggests the existence of some time or rate constraint.

Some wasps make a temporary closure on a cell either between each foraging trip (e.g., *Ammophila dysmica*, Rosenheim 1987 and references therein) or at the end of a day if the active cell has insufficient provisions to be completed (e.g., *Sceliphron caementarium*, Shafer 1949, pp. 48–53). Night-time closures must be built and then broken, which is less efficient than completing and permanently closing a cell at the end of a day. Temporary closures may also be more susceptible than final closures to break-ins by parasites, conspecific nest usurpers and cleptoparasitic species. We have found no conclusive data on the protection afforded by temporary compared with final closures, although Rosenheim (1987) has suggested that final closures provide more protection in *A. dysmica*. Females of many species may tend to complete and close cells at the end of a day or limit the period between initial provisioning and final closure; in either case the rate of foraging will influence the provisions per cell, and helpers are likely to increase foraging rate.

Second, the presence of helpers may provide greater protection from parasites. Cells may therefore be left open longer for provisioning, or primary foragers may spend less time protecting a nest. Protection from parasites by helpers has been considered one of the primary selective pressures in the origins of social behavior (Lin 1964; Michener 1974, pp. 245–248; Litte 1977; West-Eberhard 1978; Brockmann and Dawkins 1979; Abrams and Eickwort 1981). Brockmann and Grafen (in press) present data suggesting that males that guard their mates' nests increase provisions per cell by increasing female provisioning efficiency. The extra food per cell when male guards are present is associated with larger offspring and a higher proportion of daughters. Rosenheim (1987) presents detailed data on the association between parasitism and a number of aspects of nest-building in the solitary ground-nesting wasp *Ammophila dysmica*. He suggests that the probability of parasitism increases with the amount of time over which a cell is provisioned, although he presents no data on this particular point.

Third, in species that provision larvae as they develop, the rate of food delivery may be an important determinant of adult size, and this rate may increase as the number of helpers increases. Plowright and Jay (1977) found that bumble bee size depends on the rate at which larvae are fed. Allodapine bees, a group with a rich diversity of social behavior, feed their larvae as they develop (Michener 1971). Helpers may protect the nest from predators (Schwarz 1988) or increase the average rate of food delivered to each larva. Michener (1971, p. 231) noted that the number of offspring increases with helping, but he did not report the sizes of offspring.

Fourth, space for building cells or rearing offspring may be limited, so when the total amount of food available for provisioning increases, the amount of food per offspring increases. For example, the number of progeny of allodapine bees may be limited by the size of their nest, which is in a hollowed stem or twig (Michener 1971, p. 231).

In summary, the model requires that space, time, parasitism, or physiological constraints lead to a positive correlation between number of provisioners or guards and offspring size. Three species of primitively eusocial halictine bees show the expected correlation between number of provisioners and amount of food in a cell or size of offspring. (a) Knerer and Atwood (1966, p. 1263) noted that in *Halictus ligatus* "... the amount of provisions tends to increase in the cells as more workers become available for field duties." Also in *H. ligatus*, Packer and Knerer (1985) reported a strong positive correlation between the number of workers in a colony and the volume of male-producing cells; however, there was no significant relationship between worker numbers and volumes of female-producing cells (Packer, personal communication). (b) From lab observations of provisioning and oviposition, Batra (1964) suggested that progeny of *Lasioglossum (Dialictus) zephyrum* were larger when the numbers of provisioners relative to egg layers increased. In an experimental lab study of this species, Kamm (1974) found that cell size increased with the number of provisioning bees in the nest. Offspring size is known to be strongly positively associated with cell size in many species (e.g., Klostermeyer et al. 1973; Kamm 1974; Kumar 1975; Alcock 1979; Cowan 1981; Freeman 1981). (c) Finally, in *Lasioglossum (Evylaeus) malachurum* a positive association has been found between the number of provisioning bees

at a nest and the size of cells and pollen balls (Michener 1974, pp. 96–97, citing the data of Legewie 1925).

2. Females gain more than males by being large, and mothers adjust the sex of their offspring accordingly

In Hymenoptera the fitness gains for making larger females may often be greater than for making larger males. This may occur because, with increasing size, a female's fecundity, survivorship or success in competition with other females increases more rapidly than a male's survivorship or mating success (Torchio and Tepedino 1980; Charnov et al. 1981). If females gain more than males by being large, then mothers would be expected to produce females in well-provisioned cells and males in cells with less food (Trivers and Willard 1973; Torchio and Tepedino 1980; Charnov et al. 1981). Similarly, in the allodapine bees, which feed larvae as they develop, mothers would be expected to produce females when provisions per offspring were relatively abundant.

Many species of solitary wasps (Krombein 1967), solitary bees (Klostermeyer et al. 1973; Tepedino and Parker 1983) and primitively eusocial bees (Plateaux-Quenu 1983; Packer and Knerer 1986) show a strong tendency to lay female eggs in large cells and male eggs in small ones. In all species for which data are available, adult body size shows a strong positive association with cell size (see references above), and amount of provisions is probably strongly associated with cell size (Packer and Knerer 1986). Brockmann and Grafen (in press) present detailed data from the solitary wasp *Trypoxylon politum* on amount of provisions and offspring size and sex. Their data show that well-provisioned offspring develop into large females and offspring with fewer provisions develop into smaller males.

The relationship between body size and fitness for male and female Hymenoptera is difficult to reconstruct from available data. Circumstantial evidence supports the hypothesis that females usually gain more than males by being large. For example, female size is positively correlated with foraging rate in *Cerceris arenaria* (Willmer 1985), with fecundity in *Sceliphron assimile* (Freeman 1981), and with winter survivorship in *Bombus* (Holm 1972). In greenhouse experiments with *Osmia lignaria propinqua*, Tepedino and Torchio (1982) found that size had a greater effect on female survivorship than on male survivorship, but that size had no detectable effect on female fecundity. Success in

competition among females for nest sites or, in social nests, for reproductive dominance, depends on size in many bee and wasp species (e.g., for bees, Michener 1974, p 96; Eickwort 1981, pp. 260–261; Eickwort 1986; and for *Polistes*, Haggard and Gamboa 1980). Moreover, male bees and wasps tend to engage in scramble rather than contest competition for mates (Barrows 1976; Alcock et al. 1978; Morse 1982); large male size is probably not a crucial factor in such mating systems. In a few cases in which males of solitary species regularly fight and defend territories, some males are larger than the largest females (e.g., Alcock et al. 1977a, 1977b; Severinghaus et al. 1981), whereas in most species females are typically larger than the largest males.

3. A helper gains more as a mother's brood becomes increasingly female biased

Hymenopteran females are more closely related to their sisters than to their brothers and, in the absence of inbreeding, are equally related to their sons and daughters (Hamilton 1972). Females therefore favor a more female-biased sex ratio when tending siblings than when caring for their own offspring (Hamilton 1972; Trivers and Hare 1976). In all but possibly the more advanced eusocial Hymenoptera it is likely that mothers control the sex ratio; the population sex ratio will often be more male biased than if females that helped to rear siblings were controlling the sex ratio (Trivers and Hare 1976). From the helpers' point of view there is an excess of males in the population, so these helpers will favor an extremely female-biased ratio in siblings because of the frequency-dependent aspect of selection of sex ratio (Fisher 1958).

Under the synergism model, helpers cause an increase in offspring size and therefore indirectly cause an increase in the proportion of females that selection favors their mother to produce. A response to this selection pressure, leading to a more female-biased sex ratio, will then increase the gains to helpers that rear sibs because of the relatedness asymmetry described in this condition. A causal synergism loop is established: helpers "cause" their mother to produce a greater than average proportion of daughters, which simultaneously increases the gains of sib-rearing versus nesting alone. Note that as helping spreads within a population, the population sex ratio does not necessarily become more female biased. The model states that colonies with a greater than average amount of

help are favored to produce a greater than average proportion of female progeny.

Asymmetries among the relatedness coefficients for helper-brother, helper-sister and mother-offspring have a strong effect on the inclusive fitness gains of sib-rearing compared with the gains for producing offspring. These asymmetries depend on several factors such as the number of different fathers contributing to a brood, inbreeding, and the number of reproductives in a colony (Hamilton 1972). In the transition from solitary to eusocial, relatedness asymmetries may be most affected by the number and relative contributions of fathers of a brood. If a mother mates only once, then there is a single father and daughters are more closely related to sisters than to their own offspring. Multiple mating by mothers reduces or reverses the mother-offspring versus helper-sib relatedness asymmetry. Helpers are always more closely related to sisters than brothers, although multiple mating reduces this asymmetry. In general multiple mating reduces the inclusive fitness gains for sib-rearing versus nesting alone. (See Frank 1987 for calculating relatedness coefficients under a variety of assumptions).

Sib-rearing may be favored under the synergism model even when queens mate more than once or when colonies are polygynous. There are two cases to consider. The first excludes all ecological and demographic factors and focuses solely on the selective pressures built into the synergism model. Then for most situations a necessary but not sufficient relatedness condition for the spread of sib-rearing is that a potential female helper be more closely related to her sisters than to her own offspring. For example, if the single queen in a colony mated twice, then the condition is that the two fathers contribute unequally to the brood. The second case includes ecological and demographic factors that reduce the success of lone foundresses compared with colonies with helpers. Here of course one can explain sib-rearing without appeal to our model. The synergism model may, however, be a potent force that complements other factors and facilitates a rapid evolutionary transition to higher rates of sib-rearing. In this case the only necessary and sufficient relatedness condition is that potential helpers be more closely related to female reproductive progeny produced by the colony than to male reproductive progeny. This condition will almost always be met for any number of matings per queen and any number of queens.

In a few species of primitively eusocial halictine bees, data suggest that foundresses often mate only once (behavioral observations, Barrows 1975;

Knerer 1983; and electrophoretic data, Crozier et al. 1987). Sperm counts also suggest that some species of bumble bees mate only once (data and references in Morse 1982). However, multiple mating occurs in several species (see reviews by Page and Metcalf 1982; Cole 1983; Starr 1984; Page 1986). Multiple egg-layers (polygyny) appear to be common in some primitively social groups (West-Eberhard 1978; Eickwort 1981; Packer 1986). The relative frequency of matrifilial (one queen) versus semisocial (polygynous) origins of eusociality is an open question (e.g., Hamilton 1972; Lin and Michener 1972; Alexander 1974; West-Eberhard 1978; Packer and Knerer 1985; Eickwort 1986; Alexander et al., in press).

Origin and spread of sib-rearing

A number of mechanisms can start the synergistic process outlined above. Daughters may initially be favored to help because of a disproportionately high level of parasitism in nests of lone females (Lin 1964; Litte 1977), or because of shortage of nest sites or other factors that reduce the success of lone foundresses (see Andersson 1984; Brockmann 1984). Or, instead of the process beginning with a little bit of helping but no sex ratio bias, there may first be a regular pattern of sex ratio variation which then favors some helping (Seger 1983; Grafen 1986). Starting with either occasional helping or sex ratio variation, the subsequent transition from solitary to eusocial may be facilitated by the synergism in our model between helping and female-biased sex ratios.

Sib-rearing, once it originates in a population, may spread and be maintained at a high frequency in the following way. Suppose that some colonies have helpers. What are the costs and benefits to a potential helper of abandoning her natal nest to found her own colony? In terms of the factors that are the focus of the synergism model, this female would suffer a reduction in inclusive fitness because without her help her natal colony would produce fewer offspring, smaller offspring, *and a higher proportion of males* (small offspring are male). This female loses both numbers of siblings and average relatedness to these siblings. These losses are offset by her gains through her own offspring. Quantitative models (unpublished) suggest that, under most circumstances, if the synergism between helping and sex ratio favors an increase in the frequency of helping when most colonies are solitary (subsocial), then these factors favor a rapid transition to most colonies having helpers;

i.e., the costs to a potential helper for nesting alone outweigh the benefits in terms of the quantities described here.

Once helping becomes frequent, subsequent modifications may enhance the further development of sib-rearing. For example, mothers may make their early daughters small so that these daughters would not be very successful as lone reproductives but could function effectively as helpers. This form of parental manipulation (Alexander 1974) may lead to sequential variation within a brood in size and sex of offspring, which is an early stage of morphological caste differentiation.

The transition from solitary to eusocial appears to be more rapid in some groups than in others, which can potentially be explained by the extent to which our model applies. Michener (1985, p. 304) comments on the relative rates of the transitions to eusociality in bees:

> It is more difficult to envision the evolution from solitary to eusocial in Halictini than in the xylocopine-apid complex because halictine nests are usually inhabited either by solitary or by eusocial bees. Selection for eusocial attributes in Halictini must be sufficiently strong to associate the various features of each morph and also to carry the process to fixation so that populations and species quickly become characterized by the existence of the morphs, i.e., by eusociality.

The trends in halictine social evolution seem generally consistent with several of the conditions and predictions of our model. Halictine bees are particularly likely to meet one critical condition of our model that may be called into question – that workers will influence the size or vigor (fitness) of individual progeny, probably by increasing provisions per cell. These bees have a tendency to lay an egg at a particular time each evening (Batra 1968), so that the rate of provisioning is likely to determine food per cell. Also, Batra (1966) found that completed cells tend to have fewer provisions when food is relatively scarce, suggesting that the colony's rate of provisioning influences the amount of provisions per cell.

Predictions and tests of the synergism model

The synergism model predicts, during the transition from solitary life to eusociality, a positive association in nests *within* populations between the the amount of help and relatively female-biased sex ratios. Other models make the same prediction. For example, in Seger's (1983) bivoltine model, the extra females produced by the mother in certain seasons facilitate ("cause") the evolution of helping by adult daughters during these seasons. There will be an association between helping and female bias under Seger's model, but helping does not causally increase the proportion of females that the mother is expected to produce, as in our model. Experimental removal of helpers in the field or manipulations of helper numbers in the lab could be used to measure the causal effect of helpers on the sex ratios produced by mothers. A model that presumes one-way causality (e.g., Seger's) can therefore be separated from our synergism model. Species that have a long history of stable eusociality are less likely to meet the prediction that helpers have a causal influence on colony sex ratio indirectly through foraging efficiency and offspring size; other selective pressures may have altered the interactions between sib-rearing and sex ratios that were important during the period of evolutionary transition.

Direct influence on the sex ratio by helpers is another potentially confounding factor. Our model requires that sex ratio shifts associated with helpers be mediated through maternal influence on offspring sex in response to (expected) offspring size or vigor. Direct worker control of sex ratio versus indirect influence of workers through their mother can be contrasted by measuring sex and size of reproductive offspring for colonies with and without help. If the relationships between sex and size are similar for the two types of colony, then maternal control can be inferred; if reproductive females are smaller in colonies with help, then a direct influence of workers on sex ratio is implicated.

We have found no field studies that measure variations in sex ratio, offspring size and sib-rearing. However, a lab study of *Halictus scabiosae* has yielded observations that are consistent with the conditions and prediction proposed by the synergism model (Knerer and Plateaux-Quenu 1967). These authors found that 23 isolated foundresses produced only males, whereas a nest with two foundresses, in which each foundress collected pollen, produced nine large females and a few small males. They also reported that a lone foundress which had amassed five relatively small pollen balls produced five sons. This same foundress was later joined by a second female. The original foundress then provisioned seven larger pollen balls and produced all daughters, even though the second female did not collect pollen. The observation that this foundress switched from making males to making females suggests that some or all of the other male-producing foundresses had mated.

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