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Haplodiploidy and the Evolution of the Social Insects

The unusual traits of the social insects are uniquely explained by Hamilton's kinship theory.

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In 1964 Hamilton (*1*) proposed a general theory for the way in which kinship is expected to affect social behavior. An important modification of Darwin's theory of natural selection, it specified the conditions under which an organism is selected to perform an altruistic act toward a related individual. It likewise specified the conditions under which an individual is selected to forego a selfish act because of the act's negative consequences on the reproductive success of relatives. Broad in scope, the theory provided an explanation for most instances of altruistic behavior, and it promised to provide the basis for a biological theory of the family.

Although many facts from diploid organisms (and some quantitative data) are explained by Hamilton's theory (*2–4*), the theory has received its main support from the study of the social insects, in particular the social Hymenoptera (ants, bees, wasps). Because species of the Hymenoptera are haplodiploid (males, haploid; females, diploid), there exist asymmetries in the way in which individuals are related to each other, so that predictions based on these asymmetries can be tested in the absence of quantitative measures of reproductive success. A set of such predictions has been advanced (*1, 5, 6*), but heavy reliance on pairwise comparisons of degrees of relatedness has obscured some of the more striking implications of haplodiploidy. These emerge when kinship theory is combined with Fisher's sex ratio theory (*7–9*) in such a way as to predict, under a variety of conditions, the ratio of investment in the two sexes, a social parameter which can be measured with sufficient precision to test the proposed theory. Such a test leads us, in turn, to a new theory concerning the evolution of worker-queen relations in the social Hymenoptera. If the work we describe is approximately valid, it lends support to the view that social behavior has evolved not only in response to a large array of ecologically defined selection pressures (*4, 5, 10*) but also according to some simple, underlying social and genetical principles.

Hamilton's Kinship Theory

An altruistic act is defined as one that harms the organism performing the act while benefiting some other individual, harm and benefit being measured in terms of reproductive success (RS). Genes inducing such behavior in their bearers will be positively selected if the recipient of the altruism is sufficiently closely related so that the genes themselves enjoy a net benefit. The conditional probability that a second individual has a given gene if a related individual is known to have the gene is called the degree of relatedness, or r (*11*). For natural selection to favor an altruistic act directed at a relative, the benefit of the act times the altruist's r to the relative must be greater than the cost of the act. Likewise, an individual is selected to forego a selfish act if its cost to a relative times the relevant r is greater than the benefit to the actor. The rules for calculating r's are straightforward in both diploid and haplodiploid species, even under inbreeding (*12*). If in calculating the selective value of a gene one computes its effect on the RS of the individual bearing it and adds to this its effects on the RS of related individuals, devalued by the relevant r's, then one has computed what Hamilton (*1*) calls inclusive fitness. Kinship theory asserts that each living creature is selected to attempt throughout its lifetime to maximize its own inclusive fitness.

In sexually reproducing species the offspring's inclusive fitness and the parent's are maximized in similar, but not identical, ways (*1, 6, 8*). This has the obvious consequence that parent and offspring are expected to show conflict over each other's altruistic and egoistic tendencies. Neither party is expected to see its interests fully realized, and data on both the existence and form of parent-offspring conflict appear to support this view (*6, 8, 13*). Since a human being typically grows to maturity dependent on a family whose members divide among themselves many resources critical to reproduction, the processes of human psychological development are expected to be strongly affected by kin interactions and designed strongly to affect such interactions. For this reason, kinship theory appears to be a necessary component of any functional theory of human psychological development.

Degrees of Relatedness in Haplodiploid Species

The social Hymenoptera account for nearly 2 percent of all described animal species, and they are characterized by a series of unusual traits. (i) They display extreme forms of altruism through the repeated evolution of sterile or near-sterile castes of workers. These workers typically help their mothers to reproduce (eusociality), but sometimes work for their sisters (semisociality) (*14*) or less related

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individuals. (ii) The altruism is sex limited: only females are workers, all males are reproductives. (iii) There are striking lapses of altruism, especially worker-queen conflict over the laying of male-producing eggs and worker-male conflict over the amount of investment males receive. (iv) All species are haplodiploid, that is, females develop from fertilized eggs and are diploid, while males develop from unfertilized eggs and are haploid. Hamilton (*1*) was the first to realize that all four traits might be related and that haplodiploidy could be used to explain the other three. Especially in his 1972 article (*6*) he demonstrated how 200 years of scientific work on the social insects stood to be reorganized around his kinship theory.

In haplodiploid species every sperm cell produced by a male has all his genes, while each egg produced by a female has (as in a diploid species) only half of her genes. Because any daughter of a male contains a full set of his genes, sisters related through both parents are unusually closely related ($r = 3/4$). The most important *r*'s, under outbreeding, are summarized in Table 1. By pairing relationships that differ in *r*, a number of predictions have been advanced, and some of these seem at first to explain the unusual traits of the social Hymenoptera. (i) A female is more related to her full sisters than she is to her own children, she "therefore easily evolves an inclination to work in the maternal nest rather than start her own" (*6*). (ii) By contrast, a male is more related to his daughters ($r = 1$) than to his siblings ($r = 1/2$). "Thus, a male is not expected to evolve worker instincts" (*6*). (iii) A female is more related to her own sons than to her brothers. "Thus, workers are expected to be comparatively reluctant to 'work' on the rearing of brothers, and if circumstances allow, inclined to replace the queen's male eggs with their own" (*6*). Since females are more closely related to their sisters than to their brothers, they are expected to be "more altruistic in their behavior toward their sisters and less so toward their brothers" (*5*).

That this system of pairwise comparisons needs refinement is apparent when both sexes are treated together. For example, a female is related to her sisters by 3/4, but she is related to her brothers by only 1/4; if she does equal work on the two sexes, as expected under outbreeding (*6, 9*), then her average effective *r* to her siblings (1/2) is the same as that to her offspring. In short, haplodiploidy in itself introduces no bias toward the evolution of eusociality. For this reason, Hamilton (*6*) added the requirement that "the sex ratio or some ability to discriminate allows the worker to work mainly in rearing sisters," and he pointed out that inbreeding should be accompanied in haplodiploid species by female-biased sex ratios [or, better put, by female-biased ratios of investment (*9*)]. As long as *F*, the inbreeding coefficient, is larger than 0, a female is more related to a daughter than to a son by a factor of $(1 + 3F)/(1 + F)$, so that she is selected to produce a similarly biased ratio of investment (*6*). Since this unique effect of inbreeding does not render eusociality more likely—a female's average effective *r* to her siblings remains, under inbreeding, the same as that to her offspring (*15*)—we suggest that Hamilton's requirement be amended to read: the asymmetrical degrees of relatedness in haplodiploid species predispose daughters to the evolution of eusocial behavior, provided that they are able to capitalize on the asymmetries, either by producing more females than the queen would prefer, or by gaining partial or complete control of the genetics of male production. The logic for this requirement is given below, along with some of its consequences.

Table 1. Degrees of relatedness between a female (or a male) and her (or his) close relatives in a haplodiploid species, assuming complete outbreeding. For the effects of inbreeding see Hamilton (*6*).

Relation	Female	Male
Mother	1/2	1 } av. = 1/2
Father	1/2	0
Full sister	3/4 } av. = 1/2	1/2
Brother	1/4	1/2
Daughter	1/2	1 } av. = 1/2
Son	1/2	0

Capitalizing on the Asymmetrical Degrees of Relatedness

In haplodiploid species, a female is symmetrically related to her own offspring (by sex of offspring) but asymmetrically related to her siblings, while a male is symmetrically related to his siblings but asymmetrically related to his own offspring. It is the male parent and the female offspring who can exploit the asymmetrical *r*'s (for personal gain in inclusive fitness); but there is not much scope for such behavior in males (*16*), while the females can exploit the *r*'s by investing resources disproportionately in sisters compared to brothers or by investing in sisters and sons (or sisters and nephews) instead of sons and daughters.

1) *Skewing the colony's investment toward reproductive females and away from males.* Imagine a solitary, outbred species in which a newly adult female can choose between working to rear her own offspring and working to rear her mother's (but not both). Assuming that such a female is equally efficient at the two kinds of work, she will enjoy an increase in inclusive fitness by raising siblings in place of offspring as long as she invests more in her sisters than in her brothers—thereby trading, so to speak, *r*'s of 1/4 for *r*'s of 3/4. For example, by working only on sisters instead of offspring, her initial gain in inclusive fitness would be 50 percent per unit invested. Were this altruism to spread such that all reproductives each generation are reared by their sisters, in a ratio controlled by the sisters, we expect three times as much to be invested in females as in males, for at this ratio of investment (1 : 3) the expected RS of a male is three times that of a female, per unit investment, exactly canceling out the workers' greater relatedness to their sisters. Were the mother to control the ratio of investment, it would equilibrate at 1 : 1, so that in eusocial species in which all reproductives are produced by the queen but reared by their sisters, strong mother-daughter conflict is expected regarding the ratio of investment, and a measurement of the ratio of investment is a measure of the relative power of the two parties (*17*).

2) *Denying to the queen the production of males.* Imagine a solitary outbred species in which a newly adult female can choose between working to rear some of her own offspring and some of her mother's. Other things being equal, she would prefer to rear sons and sisters. A second female who had to choose between solitary life and helping this sister would choose the latter, since she would then trade *r*'s of 1/2 for *r*'s of 3/4 and 3/8. The mother would benefit by this arrangement, since she would gain daughters in place of granddaughters, but she would benefit more if she could induce daughters to work for her without producing any sons of their own, so that strong worker-queen conflict is expected over who lays the male-producing eggs.

Likewise, there should be conflict between the workers over who produces male eggs, but such conflict is expected to be less intense than similar sister-sister conflict in diploid species. Were the arrangement to spread, such that in each generation all female reproductives are daughters of the queen and all males are her grandsons (by laying workers), then if the nonlaying workers control the ratio of investment, we expect a 1 : 1 ratio. Although a worker is twice as related to a sister (3/4) as to a nephew (3/8), a male is in turn twice as valuable, per unit investment, as a female reproductive. This is because he will father female reproductives ($r = 1$) and males (by a laying worker) ($r = 1/2$), while a female will (like her mother) produce female reproductives ($r = 1/2$) and males by laying workers ($r = 1/4$). Since $(3/4)(1/2 + 1/4) = (3/8)(1 + 1/2)$, the workers' preferred ratio of investment is 1 : 1 (*18*). It is trivial to show that a queen also prefers a 1 : 1 ratio of investment, but if laying workers control the ratio of investment, then we expect a 4 : 3 ratio (since a laying worker is related to her sons by 1/2 and to her sisters by 3/4). The important general point to bear in mind is that laying workers introduce an extra meiotic event into the production of males, and this extra event automatically raises the value of a male relative to a female reproductive.

3) *The intermediate cases.* When some fraction, p, of the males in each generation is produced by the queen, and the remainder, $1 - p$, by laying workers, then the equilibrial ratios of investment can be calculated as long as one assumes that p remains relatively constant from one generation to the next and that within a colony individuals prefer to allocate resources to the two sexes according to their average r to members of the two sexes. With these two assumptions, it is relatively easy to show (*19*) that under queen control the equilibrial ratio of investment, x, results when

$$x = \frac{(3 - p)(1 + p)}{(3 + p)}$$

while under worker control it results when

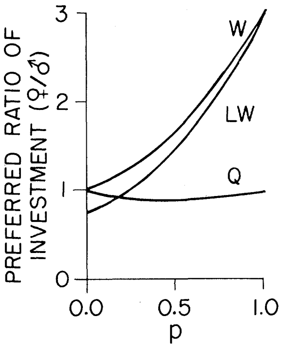
$$x = \frac{(3 - p)^2}{3(3 + p)}$$

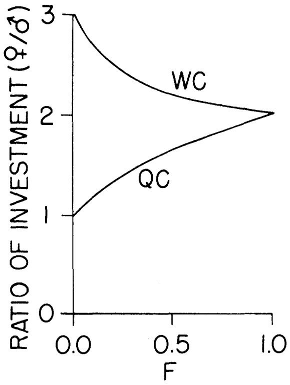
and under laying worker control when

$$x = \frac{2(3 - p)(2 - p)}{3(3 + p)}$$

The three competing optimums are presented in Fig. 1. Even if the queen produces as few as one-third of the males, there is a substantial difference between expected ratios depending on who is assumed to control that ratio. Once the queen produces at least two-thirds of the males, workers prefer a ratio of investment of at least 1 : 2.

4) *The effects of inbreeding.* The above considerations are modified slightly under inbreeding. As long as $F < 1$, the relevant r's remain asymmetrical so that daughters can exploit them as they can under outbreeding. But inbreeding does reduce the asymmetries so that the payoffs associated with the various options become more alike as F approaches 1 (*6*). This means that the higher the value of F, the less likely is the evolution of eusocial behavior. At $F = 1$ and $p = 1$ (that is, complete inbreeding and complete maternal control of male egg production), both the workers and the queen prefer 1 : 2 ratios of investment, and no conflict is expected over any of the colony's activities. For $p = 1$, the equilibrial ratios of investment are given as a function of differing values of F in Fig. 2. The important point regarding ratios of investment is that such ratios are never expected to be more female biased than 1 : 2 on the effects of inbreeding alone. All values between 1 : 2 and 1 : 3 must reflect worker performances for sisters over brothers. Values more female biased than 1 : 3 are only expected where extreme patterns of dispersal occur (*9*).





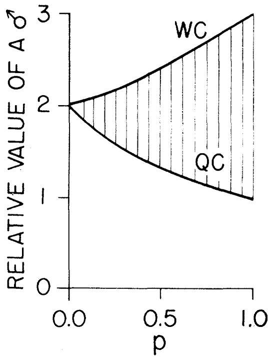


Fig. 1 (left). The preferred ratio of investment within eusocial Hymenoptera colonies for the three interested parties, the queen (*Q*), a laying worker (*LW*), and the nonlaying workers (*W*), as a function of the fraction of male-producing eggs laid by the queen (*p*), where the remainder are laid by a single laying worker. Note that queen-worker disagreement over the ratio of investment increases as *p* approaches 1. Fig. 2. (center). The equilibrial ratio of investment as a function of inbreeding coefficient, *F*, assuming that the queen lays all of the male-producing eggs. Abbreviations: *QC*, queen control of the ratio of investment; *WC*, worker control. Fig. 3 (right). The relative value of a male (based on his expected genetic contribution to future generations) compared to the value of a female, per unit investment, as a function of *p*, depending on whether the queen controls the ratio of investment (*QC*), the nonlaying workers control the ratio of investment (*WC*), or the ratio of investment is jointly controlled (shaded area). Only under the unlikely assumption of complete queen control of the ratio of investment (and male production) is the value of a male, per unit investment, equal to that of a female.

Although Hamilton has given us an admirable treatment of the possible role of inbreeding in the evolution of the social Hymenoptera (*6*), we believe its usual role has been negligible, so that the assumption of outbreeding is usually valid. Because the strong selection pressures for producing diverse young act against inbreeding in the same way in which they act against parthenogenesis (*20*), outbreeding should, like sexual reproduction, have strong positive value in most species. In addition, outbreeding is more easily associated with eusociality than is inbreeding, so that the solitary Hymenoptera should typically show larger values of F than the social species. Most of the evidence we shall later present is consistent with this view of inbreeding.

5) *The early evolution of eusociality.* Imagine for a moment that daughters are unable to reproduce within their mother's nest, so that they can choose between working there and rearing their own offspring. As pointed out above, they should naturally choose to work for their mother as long as they can preferentially invest in their sisters. Of course the spread of such a preference for sisters should naturally lead to a female-biased ratio of investment, and such a biased ratio raises the value of males, thereby altering the payoffs associated with the daughters' options. The precise genetical analysis is both tedious and complex. Instead, by imagining that the ratio of investment in our incipiently eusocial species is undergoing a steady change, it is easy to give an approximate outline of the relevant selection pressures.

Initially, a female-biased ratio of investment favors mothers who increase the number of their sons, but such behavior should select for workers who respond to sex ratios facultatively, working only when their mothers agree, in effect, to specialize in the production of daughters. As the ratio of investment passes the 1 : 1.5 mark, a selection pressure appears for workers to work on sons rather than sisters, either on their own or (if we relax our initial requirement) within the maternal nest. If this does not stop the biasing process, the ratio of investment may pass 1 : 2 at which point workers are favored to concentrate on nephews in preference to sisters, intensifying selection for a return to less biased ratios. In short, one never expects a 1 : 3 ratio of investment as an early consequence of a eusocial trend. Instead, one expects that a polymorphism will naturally develop; some large, strifeless nests will specialize in the production of female reproductives and many solitary and small semisocial nests will specialize in the production of males. Such a polymorphism gives to eusocial colonies the evolutionary time to evolve the efficiencies which may eliminate entirely solitary nests in favor of large nests which produce the female reproductives and all the males by a mixture of queen and laying worker contributions.

A second consequence of the imagined early polymorphism is the sharp reduction in the value of males produced in the previous generation. Imagine that fertilized queens overwinter singly and begin new nests in the spring. Some produce daughters who are destined to remain with their mothers to work on rearing female reproductives. Others produce daughters destined to produce sons of their own. Because males are produced from unfertilized eggs, the polymorphism has rendered males superfluous in the first spring generation. As long as the spring queens typically live long enough to produce all the female reproductives, no new sperm is required in the spring and hence all queens can concentrate on the production of daughters to the virtual exclusion of sons. This trivial consequence of haplodiploidy is well documented for so-called primitively eusocial bees (see below).

6) *Summary.* It appears that there are two, partly overlapping ways by which haplodiploid daughters may be expected to evolve eusocial behavior. Either of these ways tends to bias the ratio of investment toward females, so that this theory can be tested by finding out whether ratios of investment in the eusocial Hymenoptera are typically female biased compared to such ratios in the solitary Hymenoptera. So far as we know, no other theory makes this prediction. In addition, under certain conditions 1 : 3 ratios are expected to be fairly common, so that more precise predictions can be tested along with the main effect. If inbreeding is usually a minor factor, then the most important variable to know is the relative power of the queen and the workers to affect the two parameters over which disagreement is expected: the frequency of laying workers and the ratio of investment.

Fundamental Bias by Sex in Social Behavior of Hymenoptera

With the analysis developed in the previous section, it is possible to present a consistent set of predictions regarding social behavior in haplodiploid species. The most important predictions, along with some of the relevant evidence, are presented here.

1) If and only if workers are assumed to be able to capitalize on the asymmetrical r's in haplodiploid species, does one expect in these species a bias toward eusociality (the evolution of worker castes). If females do not respond appropriately to the asymmetrical r's, then their average effective r to their siblings will be the same as that to their own offspring. But if they respond in either of the two ways outlined above, their average r to their siblings will rise above that to their offspring. In short, a bias toward eusociality in the haplodiploid Hymenoptera is contingent upon the discriminatory capacities of the workers. The expectation of this bias does not depend on the assumption that the first workers showed appropriate discriminatory behavior; as long as workers evolved such behavior, their working was more likely to remain adaptive (in the face of fluctuating conditions). Once eusociality appears, it is more likely to endure in haplodiploid than diploid species.

Although species of diploid insects are apparently far more numerous than species of haplodiploid insects, eusociality has evolved only once (the termites) in diploid insects but more than 11 times independently in the Hymenoptera (*5, 10*). Incipient eusociality, in which an individual helps its parents for one or more years but not usually for life, has evolved repeatedly in mammals but with no bias toward female helpers. In birds, helpers at the nest are usually, but not always, males (*21*), presumably because the expected RS of a young male is typically less than that of his same-aged sister (*22*). Helpers in social carnivores may be male or female (*23, 24*).

2) The same bias toward eusociality can be demonstrated assuming multiple insemination of the queen (compared to multiple insemination in diploid organisms). If the queen is inseminated twice equally, then the average r between a female and her sister will be 1/2 and between a female and her brother, 1/4. The average of these two will be 3/8, which is the same average r between siblings in a diploid species, given the same pattern of insemination. For any multiple insemination, it is trivial to show that a female's average r to her siblings is the same in haplodiploid as in diploid species. But females can still capitalize on the asymmetrical r's. Multiple inseminations remove this possibility only if each daughter is fathered by a different, unrelated male, and if workers are unable to produce any sons. (This same extreme requirement is necessary if the predictions that follow are also to be invalidated through multiple inseminations.) It is, of course, obvious that multiple inseminations render the evolution of worker habits less likely in both haplodiploid and diploid species.

No data exist which would permit one to compare the frequency of multiple inseminations in diploid and haplodiploid insects. What data exist suggest that multiple insemination is infrequent in both groups. In addition, it appears likely that multiple insemination has evolved in the social Hymenoptera as a response to eusociality: a social insect queen may produce tens of millions of workers in her lifetime, overtaxing the spermatogenic capacity of a single male (*1, 25*). As long as there is a tendency for sperm to clump according to father, as expected (*26*), there will be a tendency, despite the multiple insemination, for r's between sisters within a colony at any moment to be near 3/4. The important point is that multiple insemination should not be treated as an independent parameter.

3) Females are more likely to evolve worker habits than are males. Once females evolve worker habits, a strong bias against the evolution of male workers at once develops. In addition, there develops a bias against males investing in their offspring. A male is unable to exploit the asymmetrical r's to his own advantage. He is equally related to his brothers as to his sisters, so he gains nothing by the overproduction of either sex. Likewise, he is unable to produce eggs himself. Since in haplodiploid species a male is no more related to his mate's offspring than to his own siblings, no initial bias in such species (compared to diploid species) is expected either toward or away from male worker habits. (A slight degree of inbreeding introduces a slight bias against male workers.) Female workers are expected to exploit the asymmetrical r's and once they do so, in either of the two available ways, the expected RS of a male rises relative to that of a reproductive female, so that the evolution of male workers becomes relatively less likely. If, for example, all males arise from worker-laid eggs, then the expected RS of a male (per unit investment) is twice that of a reproductive female, so that a male would have to be more than twice as effective a worker (gram for gram) as a female in order for selection to favor his helping in the nest (*27*). In general, when the ratio of investment is controlled by the workers, a male's expected RS is $6/(3 - p)$ times that of a reproductive female (where p is the fraction of males that come from queen-laid eggs). If the ratio of investment is completely controlled by the queen, then the male's expected RS per unit investment is $2/(1 + p)$ times that of a female. For both worker and queen control of the ratio of investment, and for all intermediate cases, the relative RS of a male is given in Fig. 3. Only under the unlikely condition of complete queen domination of

both male production and the ratio of investment is the expected RS of a male equal to that of a female. Under all other conditions the greater expected RS of a male makes helping behavior and altruism relatively unlikely. In addition, except under complete, or near complete, queen control of the ratio of investment, male parental investment becomes less likely, since a male is expected to inseminate more than one female (per unit investment in him).

In contrast to the termites (all species of which have both male and female workers), there are no species of Hymenoptera that have castes of male workers (*5*). Indeed, with one or two exceptions (*5, 28–31*), males have never been seen to contribute anything positive to the colony from which they originate. Again in contrast to the termites, males from social species of Hymenoptera have never been seen to contribute to the colonies that result from their sexual unions, yet rudimentary male parental investment occurs in some solitary species of Hymenoptera (*32, 33*).

4) No matter who produces the males or who controls the ratio of investment, greater conflict is expected between the workers and the males than between the workers and the reproductive females. Such worker-male conflict is expected to be especially intense where workers control the ratio of investment. If the queen produces all of the males and also controls the ratio of investment (at 1 : 1), then workers are expected to value their sisters three times as much as their brothers, while each male and each reproductive female values itself twice as much as other reproductives (averaging males and females). Males will then have to work harder to gain appropriate care than will reproductive females. Of course, worker preferences for sisters ought inevitably to lead to a biased ratio of investment. If workers gain their preferred ratio of investment (as a function of p), then they will value reproductives of the two sexes equally; but a male will value himself more relative to his siblings than will a reproductive female relative to her siblings (by approximately the amount shown in Fig. 3) (*27*), so that selection will more strongly favor male efforts (compared to female efforts) to gain more investment than workers are selected to give, leading to increased worker-male conflict. The argument extends to the intermediate situations as well, but worker-male conflict should be most intense under worker control of the ratio of investment (Fig. 3).

Male-worker conflict appears to be widespread in the social Hymenoptera. For example, male *Mischocyttarus drewseni* mob workers more intensely than do female reproductives, and males are more selfish in their behavior toward larvae (*31*). Shortly after they eclose, males may be chased from the nest (and killed if they resist), while females are fed in both *Polistes* and *Bombus* (*34*). In times of food shortage *Camponotus* workers first cannibalize males before turning to female reproductives (*28*). *Tetramorium* males are apparently starved after they eclose while reproductive females are intensively fed (*35*).

5) Either laying workers, or a biased ratio of investment in the reproductives, or both, are expected in all eusocial Hymenoptera. Where there are no laying workers, the ratio of investment is expected to approach 1 : 3 (male to female). In other species, the ratio of investment is expected to correlate with p. For reasons outlined earlier, it will be beneficial to the workers if they can produce some or all of the males (but none of the females) or if they can bias the ratio of investment toward their reproductive sisters. Although it is advantageous for the queen to prevent both of these possibilities, there is no reason to suppose that the queen can completely override the maneuvers of her daughters. In the absence of laying workers, one expects a ratio of investment biased toward 1 : 3. As shown earlier, the lower the proportion (p) of males who come from queen-laid eggs, the more nearly the nonlaying workers prefer a 1 : 1 ratio of investment.

A number of species are known to have laying workers (*1, 5, 6*) but the contribution of these laying workers to the total of males is usually unknown, and most species remain completely unstudied in this regard. It is sometimes supposed that workers must lay male-producing eggs (if they lay any) since they are assumed to be unfertilized, but it is preferable to argue that they remain unfertilized because there is usually no gain in being able to produce daughters. Even wingless, workerlike female ants are fertilized in species lacking winged queens (*36, 37*), and in some primitively eusocial bees a significant percentage of workers are regularly fertilized; yet fertilized workers have well-developed ovaries no more often than do unfertilized workers (*38*), suggesting the absence of a selection pressure to produce daughters when the queen is functioning. The ratio of investment in eusocial Hymenoptera is discussed below.

6) The early evolution of eusociality should be characterized by the lengthening of the queen's life so as to produce several generations. Males are expected to be infrequent in the early generations and frequent during the queen's terminal generation. The early evolution of eusociality should be characterized by a polymorphism in which some nests consist of queens and their daughters specializing in the production of female reproductives and other nests consist of daughters, singly or in small groups, producing male reproductives. Such a social grouping actually consists of two generations (in addition to the queen): the generation of adult workers and the generation of adult reproductives whom they rear. If all queens survive to produce the female reproductives, then there will be no value to any males produced along with the generation of workers. Of course, additional generations of workers can be inserted, so that an early eusocial hymenopteran species easily comes to resemble the summer parthenogenetic generations of aphids culminating in the fall production of sexuals.

The correlations proposed are among the most clear-cut in the detailed literature on the early evolution of eusociality in bees (*10*). For example, the series of eusocial halictine bees, *Lasioglossum zephyrum, L. versatum, L. imitatum*, and *L. malachurum*, shows "progressively increasing differences in size and in ovarian development between castes, decreasing frequency of worker mating, increasing queen longevity, and decreasing spring and early summer male production" (*39*).

7) A bias toward the evolution of semisociality (females helping their sister raise her offspring) is expected in haplodiploid species (compared to diploid species). A haplodiploid female is related to her sister's offspring by $r = 3/8$ and to her own by $r = 1/2$, while a diploid female is related to her sister's offspring by $r = 1/4$ and to her own by $r = 1/2$, so that, other things being equal, semisociality is more likely in haplodiploid than diploid species. As with eusociality, the bias still persists even if the female is inseminated more than once, as long as each of her daughters is not inseminated by a different male. A male is related to his sibling's offspring by $r = 1/4$ and to his mate's by $r = 1/2$, so that he is less likely to evolve semisocial habits than are his sisters, but no less likely than males in diploid species. No biased ratio of investment is expected in purely semisocial species.

Semisocial habits (involving females) have evolved independently in the Hymenoptera even more often than have eusocial habits (*5*), yet they have not evolved, so far as is known, in the diploid insects. No semisocial behavior is known in haplodiploid males, but their adult behavior is virtually unstudied. Semisocial habits have evolved several times in birds and mammals, more commonly among brothers than among sisters (*2, 23, 40*).

Ratio of Investment in Monogynous Ants

In the system outlined above, the critical prediction is that workers will bias the ratio of investment toward females whenever some or all of the males come from queen-laid eggs. Since in ants workers feed and care for the reproductives from the time the reproductives are laid as eggs until they leave the nest as adults and since there are usually hundreds of workers (or more) per queen, it is difficult to see how an ant queen could prevent her daughters from producing almost the ratio of investment that maximizes the workers' inclusive fitness. In some ants, such as *Atta* and *Solenopsis* (*5*), all males appear to be produced by the queen, and in other monogynous ants (single queen per nest) laying workers appear to be a relatively uncommon source of males (compared to eusocial bees and wasps) (*41*), so that the ratio of investment in ants should often approach 1 : 3. This prediction can be tested by ascertaining the sex ratio of reproductives (alates) commonly produced by a species and correcting these data by an estimate of the relative cost (to a colony) of a female alate compared to a male.

There exist good data on the sex ratio of alates for about 20 ant species, based on complete nests dug up during the time when alates were present in the nest. Ideally, nests should be dug up after all alate forms have pupated (since pupae can be sexed while larvae cannot) but before any of the alates have flown (since one sex may fly earlier than the other). Such data exist, primarily from the pioneering population studies of Talbot (*42*). Sex ratios so obtained do not differ from sex ratios for the same species based on all nests (*42*), so data on complete nests dug up anytime were used (*43*). The number of alates counted, the number of nests from which they came, and the sex ratio for monogynous ants (including two slave-making species) are presented in Table 2. The quality of the data (based on sample sizes) varies widely (*44*). The sex ratio varies over a 20-fold range (compare *Formica pallidefulva* and *Prenolepis imparis*).

Since in monogynous species workers invest in the reproductives almost exclusively by feeding them, the relative dry weight of a mature male and female alate was taken as a good estimate of their relative cost (*45, 46*). Dry weights for males and females and the dry weight ratio (female to male) are presented in Table 2. Multiplying the sex ratio by the dry weight ratio gives an estimate of the relative investment in the two sexes (Table 2). This estimate should be approximately valid for monogynous and slave-making species but not, as explained below, for polygynous species.

For 21 monogynous ant species, the sex ratio of alates is plotted against their relative dry weight in Fig. 4A. The points tend to scatter around the 1 : 3 line of investment instead of the 1 : 1. The data are fitted by a linear regression in which

$$y = 0.33x - 0.1$$

The slope of this line is not significantly different from a 1 : 3 slope, but it deviates in a highly significant manner from a 1 : 1 slope ($P \ll .01$). In fact, all species are biased toward investment in females, and the least biased species show a 1 : 1.57 ratio of investment. The geometric mean ratio of investment for all species is 1 : 3.45 (range 1.57 to 8.88). The scatter around the 1 : 3 line appears partly to reflect sample size. For example, five of the six species with the best data show a range of only 2.99 to 4.14 (geometric mean = 3.36) (*47*). The other species (*Acromyrmex octospinosus*) has a ratio of investment of 1.59. It is the only species with a value of p estimated to be lower than 1 ($p = 0.63$), so that its expected ratio, under worker control, is only 1.94. There is a strong inverse relationship ($P \ll .01$; t-test) between the number of males produced and the relative size

Table 2. The sex ratios of reproductives (males/females) from natural nests of 21 monogynous species of ants and two slave-making species (indicated by s), along with the mean dry weights of male and female reproductives, the dry weight ratio and the inverse of the ratio of investment (inverse of 1 : 3 ratio = 3). Blanks indicate lack of data. Weights are based on dried specimens in the collections of the Museum of Comparative Zoology, Harvard University, except where otherwise stated in the references. The mean weights are based on sample size of five individuals except where noted with the following superscripts: a = 1; b = 2; c = 3; d = 4; e = 6; f = 8; g = 9; h = 10; i = 14; j = 15; k = 20; L = 30; m = 66.

Species	Reproductives counted (No.)	Nests (No.)	Sex ratio	Weight-F (mg)	S.D.	Weight-M (mg)	S.D.	Weight ratio (F/M)	Inverse ratio of investment	Reference
				Subfamily: Formicinae						
Camponotus ferrugineus	1,854	6	1.29	41.18	7.39	6.32	0.50	6.52	5.05	(*99*)
C. herculeanus	6,300	1*	2.50	56.5^{d}	11.1	10.6^{d}	2.4	5.33	2.15	(*100*)
C. pennsylvanicus	1,249	4	0.77	59.5^{f}	11.5	8.7^{c}	3.3	6.84	8.88	(*99*)
Formica pallidefulva	2,278	31	0.44	14.4^{c}	1.7	7.9^{c}	1.2	1.82	4.14	(*101*)
Prenolepis imparis	1,994	11	8.36	12.7^{L}		0.50^{g}		25.4	3.04	(*102*)
				Subfamily: Myrmicinae						
Acromyrmex octospinosus	4,490	10	0.9	19.66^{b}	3.5	7.87	2.74	2.50	2.78	(*103*)
Aphaenogaster rudis	361	14	5.45	6.1^{j}		0.48^{j}		12.71	2.32	(*104*)
A. treatae	2,024	12	1.55	9.1^{f}		0.9^{f}		10.1	6.52	(*105*)
Atta bisphaerica	35,249	5	3.18					8.00	2.52	(*106*)
A. laevigata	22,723	6	2.87	263.9^{a}		31.5	2.7	8.37	2.91	(*106*)
A. sexdens	119,936	7	4.90	264.7^{h}	100.8	34.5^{h}	9.6	7.67	1.57	(*106*)
Harpagoxenus sublaevis (s)	2,459	58	1.38	0.59^{L}		0.34^{L}		1.73	(1.25)s	(*36, 55*)
Leptothorax ambiguus	169	12	0.82	0.63^{d}		0.10^{k}		6.30	7.68	(*56*)
L. curvispinosus	1,113	82	1.40	0.68^{L}		0.15^{L}		4.53	3.24	(*57*)
L. duloticus (s)	1,620	96	2.31	0.20		0.10		2.0	(0.87)s	(*54*)
L. longispinosus	206	12	0.62	0.54		0.11^{e}		4.90	7.90	(*56, 57*)
Myrmecina americana	226	10	1.19	0.55^{d}		0.21^{d}		2.62	2.20	(*56*)
M. schencki	795	10	0.31	2.0^{d}		1.0^{f}		2.00	6.45	(*107*)
M. sulcinodis	1,114	21	1.15	2.2	0.29	1.2	0.10	1.83	1.59	(*108*)
Solenopsis invicta	200,491	†	1.00	7.4^{g}		2.1		3.52	3.52	(*50*)
Stenamma brevicorne	235	10	0.90	0.88^{d}	0.06	0.36^{d}	0.09	2.44	2.71	(*56*)
S. diecki	391	9	1.30	0.52^{c}	0.06	0.15^{c}	0.01	3.46	2.66	(*56*)
Tetramorium caespitum	73,389	126	1.34	6.0		1.5		4.00	2.99	(*109*)

*Hölldobler (*28*) also estimated the sex ratio in 15 to 20 additional nests. It ranged between 2 and 3.

†Hundreds of nests (*50*).

of a male (compared to a female). This inverse relation is predicted by Fisher's sex ratio theory (*9*), and, so far as we know, these are the first data—from any group of organisms—demonstrating this relation.

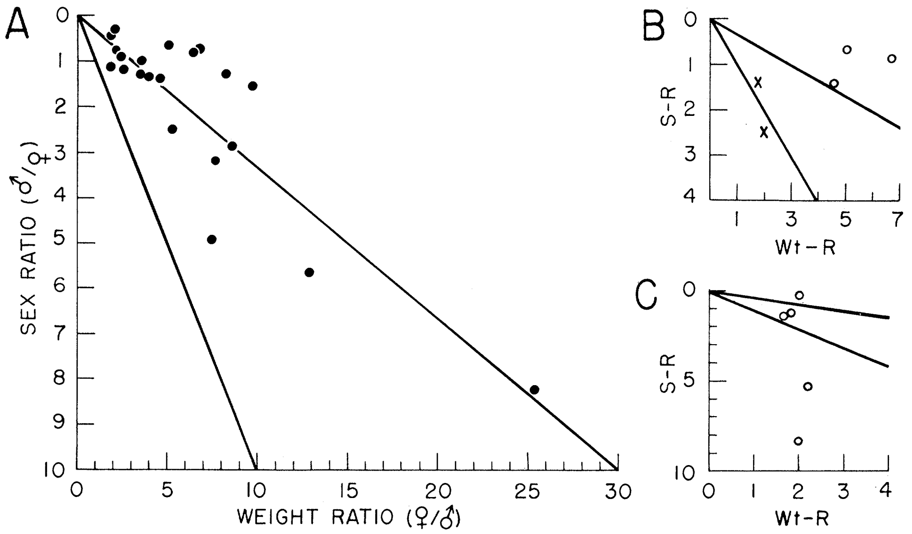


Fig. 4. The sex ratio (male/female) of reproductives (alates) is plotted as a function of the adult dry weight ratio (female/male) for various ant species (Table 2). Lines showing 1 : 1 and 1 : 3 ratios of investment are drawn for comparison. (A) All monogynous species. (B) Two slave-making species (x) and three closely related nonslave makers (*Leptothorax*). (C) Five species of *Myrmica* (from top to bottom) *M. schencki*, *M. sulcinodis*, *M. ruginodis*, *M. sabuleti*, and *M. rubra*.

It would be valuable to refine our measure of relative cost. Minor biases are expected from a number of sources. Females contain relatively less water than do males (*35, 45*), they are richer in calories per gram than are males (*35, 48*), they are larger than males and therefore consume relatively less oxygen per unit weight (*49*), and they apparently require less energy (per unit weight) during development than do males (*35*). Peakin's detailed study permits an overall estimate of the relationship between relative dry weight and relative caloric cost; for *Tetramorium caespitum*, females appear to be three-fourths as expensive as suggested by relative dry weight at the time of swarming (*35*), so that the ratio of investment based on caloric cost for this species would be 1 : 2.25 (instead of 1 : 2.98 as given in Table 2). The need for something like a three-fourths correction also appears likely from the pattern of our investment data: a mean ratio of 3.45 for all species, a mean of 3.36 for the five best studied species, and a 3.54 ratio for the single best studied species, *Solenopsis invicta* (*50*), which lacks laying workers and which is certainly typically outbred. In short, real ratios of investment in monogynous ants appear to be near 1 : 3 and certainly larger than 1 : 2.25.

To confirm the contention that the 1 : 3 ratio of investment in monogynous ants results from the asymmetrical preferences of the workers, a series of tests is possible, involving species of ants in which the workers are unrelated to the brood they rear (slave-making ants), species of ants in which winged females receive investment in addition to their body weight which males do not receive (polygynous ants), diploid species with workers (termites), haplodiploid species without workers (solitary bees and wasps), and other haplodiploid species with workers (eusocial bees and wasps). Data on the ratio of investment in these species are presented in the following sections.

Ratio of Investment in Slave-Making Ants

In slave-making ants, the queen's brood is reared not by her own daughters but by slaves, workers of other species stolen from their own nests while pupae or larvae (*5*). The slave-making workers spend their time slave-raiding, and they typically capture several times their own number in slaves. The slaves feed and care for the slave-making queen and her brood. The slaves are, of course, unrelated to the brood they rear and should have no stake in the ratio of investment they produce. The queen, as always, prefers a 1 : 1 ratio of investment, and in slave-making species she should be able to see her own preferred ratio realized (*51–53*).

The only slave-making ants for which we have found sex ratio data are *Leptothorax duloticus* (*54*) and *Harpagoxenus sublaevis* (*36, 55*), two closely related species who prey on other *Leptothorax* species. Fortunately, the data themselves are excellent, being based on large and unbiased samples, and permit a comparison with equally good data from a closely related species that is not slave-making, *L. curvispinosus* (*56, 57*), and with less detailed data from two other closely related species that are not slave-makers (Table 2). The sex ratio is plotted as a function of relative dry weight for all five species in Fig. 4B. In contrast to these three species, the ratio of investment in both slave-makers is close to 1 : 1 and the geometric mean for the two is 1.00. Each slave-maker has a lower ratio of investment than all other monogynous species shown in Table 2, a highly significant deviation ($P < .001$) toward a 1 : 1 ratio. In *L. duloticus* sexual dimorphism is reduced (through reduction in size of the female) and yet the relative number of males is increased (*58*).

Leptothorax duloticus enslaves mostly *L. curvispinosus* workers, who in their own nests produce a ratio of investment of about 1 : 3. Since the slaves eclose as adults in a strange nest and go to work caring for the brood as if it were their mother's, why do they not attempt to produce the 1 : 3 ratio of investment typical of their own nests? When *duloticus* first began enslaving *curvispinosus*, the slaves presumably produced a 1 : 3 ratio of investment in the *duloticus* nest, but selection then favored the *duloticus* queen—by whatever means—biasing the ratio of investment back toward 1 : 1, and selection did not favor any countermove by the slaves. In giving up care of the brood in order to raid for slaves, the *duloticus* workers presumably gained sufficient increase in their inclusive fitness to compensate for the loss of their control over the ratio of investment (*59*).

Ratio of Investment in Polygynous Ants

In polygynous ant species, polygynous nests arise when a queen permits one or more of her fertilized daughters to settle within her nest (*60, 61*). Large polygynous nests may contain granddaughter queens and even later generation queens. Polygynous nests introduce a bias in the sex ratio because the inclusion of reproductive daughters in the maternal nest increases the relative cost of a female reproductive compared to that of a male (*62*).

If a reproductive daughter is permitted to settle within or near the maternal nest when unrelated females would not be so permitted, then one must assume that the daughter thereby inflicts a cost on her mother (measured in terms of reproductive success) which her mother permits because of the associated benefit for the daughter. This cost can be treated as a component of investment and raises the relative cost of a reproductive female. If we assume outbreeding, the male mates with a female who forces the same cost (with its associated benefit) on her mother, so that a male gains the same benefit without inflicting a cost on his mother (*63*). In short, in polygynous ants we expect the ratio of investment, as measured by relative dry weight, to be biased toward males. This appears to be true for seven polygynous species with the appropriate data (Table 3). There are also several indications of male-biased ratios of investment in polygynous *Formica* (*64*). Likewise, two polygynous *Pseudomyrmex* have less female-biased ratios of investment than do two monogynous species (*65*). The more daughters that are permitted to settle in this fashion, the greater will be the relative cost of an individual reproductive female, so that a positive correlation is expected between the degree of polygyny (as measured by the number of queens in a typical nest) and the ratio of investment based on relative dry weight. The most interesting genus in this regard is *Myrmica* (Fig. 4C). Two species are monogynous, *M. schencki* and *M. sulcinodis*, the latter with many laying workers (Table 2). Two are polygynous, *M. rubra* and *M. sabuleti*, with 5 and 15 queens per nest, respectively (Table 3). The third species, *M. ruginodis*, is both monogynous and polygynous (Table 3) (*66*). The ratios of investment for these species are ordered exactly according to the parameters we have outlined (see Fig. 4C).

Ratio of Investment in Termites

Termites are diploid. In the absence of inbreeding, one expects all colony members, queen and king, female and male workers, to prefer equal investment in reproductives of the two sexes. This is true as long as the colony is monogynous but is not true if the queen is capable of producing some of her daughters by parthenogenesis. Unfortunately, there are almost no data on termite sex ratios and, with one exception (*67, 68*), none based on complete nests. In addition, it is difficult to get specimens to weigh. We have used two kinds of data. (i) Roonwal and his associates gathered sex ratio data, based on naturally occurring swarms, for four species and also ascertained wet and dry weights for male and female alates (*69*). (ii) Sands sampled between two and four nests for five species of *Trinervitermes* and also provided weights (*67, 70*). The data from the two sources are plotted in Fig. 5. The geometric mean ratio of investment for these nine species of termites is 1.62, which is significantly closer to 1 : 1 than are the ratios for monogynous ants ($P < .001$; *t*-test). There is no significant difference between the termite mean and that of the slave-making ants, a result consistent with the expectation that they be almost equal. However, the termite data are thin enough that they neither strongly support nor contradict our arguments.

Table 3. The sex ratio, weight ratio, and inverse ratio of investment for polygynous ant species.

Species	Sex ratio	Weight-F (mg)	S.D.	Weight-M (mg)	S.D.	Weight ratio (F/M)	Inverse ratio of investment	Reference
Crematogaster mimosae	12	4.79^{a}	0.62	0.46^{a}	0.01	10.4	0.87	(*110*)
C. nigriceps	6	2.4^{b}	0.03	0.57^{b}	0.07	4.2	0.70	(*110*)
Iridomyrmex humilis							0.1	(*111*)
Myrmica rubra	8.37	2.2	0.21	1.1^{c}	0.24	2.02	0.25	(*51, 112*)
M. ruginodis	1.11	1.87	0.29	1.14	0.18	1.61	1.45	(*66*)
Polygynous	6.71						0.24	
Monogynous	0.92						1.75	
M. sabuleti	5.18	2.2	0.08	1.0	0.23	2.20	0.42	(*51, 112*)
Pheidole pallidula	6.2	3.35		0.6		5.58	0.9	(*113*)
Tetraponera penzegi	1.8	0.93^{a}	0.01	0.48^{a}	0.10	1.94	1.1	(*110*)

a = sample size of 2; b = 3; c = 6.

Table 4. The sex ratio (males/females) from natural nests of solitary species of bees and wasps, along with adult dry weight of males and females of these species. Blanks indicate lack of data. The mean weight for each sex is based on a sample size of five with three exceptions.

Species	Offspring counted (No.)	Sex ratio	Weight-F (mg)	S.D.	Weight-M (mg)	S.D.	Reference
			Solitary bees				
Agapostemon nasutus	87	2.11	9.7	2.7	6.4	0.6	(*114*)
Anthophora abrupta	169	1.64	58.0	10.7	36.7	1.6	(*115*)
A. edwardsii	225	1.48	49.0^{a}	2.9	36.6^{a}	3.2	(*116*)
A. flexipes	200	1.50	17.3	2.6	15.1	1.5	(*117*)
A. occidentalis	241	1.06	89.7	3.7	51.1	6.3	(*118*)
A. peritomae	70	1.00	23.8^{b}	4.1	10.1	1.7	(*119*)
Chilicola ashmeadi	84	2.82	0.8	0.06	0.5	0.05	(*120*)
Euplusia surinamensis	297	1.44	148.7	18.7	123.6	31.0	(*121*)
Hoplitis anthocopoides	351	1.95	11.6	1.6	12.3	2.7	(*122*)
Nomia melanderi	500	1.01	25.5	5.5	31.9	3.3	(*123*)
Osmia excavata	2,820	1.69	24.9	4.8	16.3	1.6	(*124*)
Pseudagapostemon divaricatus	222	1.61					(*125*)
			Solitary wasps				
Antodynerus flavescens	200	1.56	22.2	2.5	14.6	2.8	(*126*)
Chalybion bengalense	183	1.47	19.6	5.9	8.7	2.8	(*126*)
Ectemnius paucimaculatus	169	1.82	4.0	1.7	3.0	1.2	(*127*)
Passaloecus eremita	114	0.70	3.4	0.9	1.6	0.3	(*128*)
Sceliphron spirifex	144	0.95					(*83*)

a = sample size of 2; b = sample size of 3.

Ratio of Investment in Solitary Bees and Wasps

In solitary (nonparasitic) bees and wasps, an adult female commonly builds a cell and provisions the cell with prey or with pollen and nectar. In each cell, she lays either a haploid (male) egg or a diploid (female) egg. In the absence of inbreeding, one expects the typical adult female to invest equally in the two sexes (*9*).

Natural nests. In most solitary bees and wasps, males emerge from and leave their nests earlier than do females (*32*). In some species the pupal stage itself is known to be shorter in males (*71*). In addition, female cells are commonly deposited first in twig-nesting species. Because of these sex differences, sex ratio data based on nests collected during the flying season are expected to be biased toward females, as indeed they appear to be (*72*). By contrast, unbiased data are expected if nests are gathered before any adults have emerged and if the contents are sexed after all larvae have pupated (since larvae can usually not be sexed). We have found such data (with a sample size of 70 or more) for 17 species (Table 4). Since we have no data on cell size or amount of provisions for individuals of either sex, we have again used relative adult dry weight as a measure of the relative cost of a male and a female. Males tend to be smaller than females and more numerous in most species sampled (Table 4). The sex ratio as a function of the dry weight ratio is plotted in Fig. 6. Although there is no tendency for relatively smaller males to be produced in relatively greater numbers, the ratio of investment in solitary bees and wasps is significantly closer to 1 : 1 than is true in monogynous ants. The geometric mean for all solitary species is 1 : 1.07. The two species which deviate most from 1 : 1 are among the three species with the smallest sample size (115 or less).

These data from natural nests can be supplemented by data from trap-nests (in which artificial nesting sites, usually holes bored in wood, are offered in the field and their contents later reared to maturity). Most such nests consist of a linear series of cells each separated by a partition of mud. The advantage of these data is that they are more numerous than natural data and they can be correlated with direct measures of the relative cost of producing the two sexes. Trap-nests may, however, introduce their own biases, for many bees and wasps prefer to produce the smaller sex (usually males) in smaller diameter holes (*73*) so that the sex ratio obtained will partly reflect the size distribution of the borings that are presented. Even where the appropriate boring sizes are offered, the data may still be biased if the size distribution of the borings does not exactly match the relative frequency of different size borings in nature. But there is no strong reason in advance to assume that trap-nests will have a systematic bias against any one sex (*74*) so that strong variance in sex ratio is expected from species to species but no systematic bias.

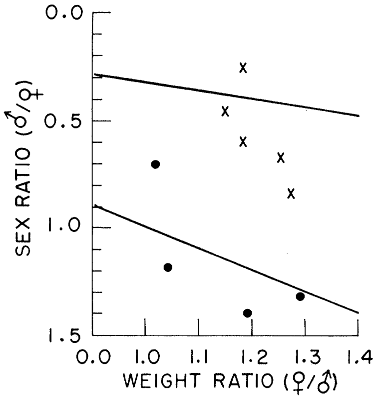


Fig. 5. The sex ratio of reproductives is plotted against the dry weight ratio for termites. Data from Roonwal *et al.* (*69*) (closed circles); data from Sands (*67, 70*) (x). The 1 : 1 and 1 : 3 lines are drawn as in Fig. 4.

Trap-nests and the measurement of relative cost. Krombein (*32*) has done the bulk of all published trap-nesting work, using the same trapping procedure in a series of localities to capture more than 100 species of solitary bees and wasps. For 27 species (Table 5) with a sample of 70 or more adults captured and reared to maturity (*75*), Krombein provided the sex of the individuals as well as their average cell dimensions. From these dimensions we have calculated the mean relative cell volume (female to male) for each species (Table 5). In addition, Krombein removed from his trap-nesting collection five typical individuals of each sex for each of the 30 species (*76*) (Table 5). We weighed the specimens and from these weights we have calculated dry weight ratios (female to male) for the same species. Comparison of these data reveals that relative volumes and relative weights are usually greater than one (females occupy more space than males and weigh more).

Since dry weight is partly a measure of the amount of food given and cell volume is a direct measure of the space allotted (*77*), the relative cell volume and the relative weight of the two sexes (female to male) can be considered partly independent measures of the substitution value of a female (in units of males). In addition, since Krombein's impression is that male and female cells were both stuffed full with prey (*78, 79*), relative cell volume is probably a good measure of relative amount of food provided. As would be expected, relative dry weight and relative volume are highly correlated, but there is a systematic tendency for females to weigh more than would be expected on the basis of cell volume (Table 5). That this discrepancy is real was confirmed by comparing the weights of our specimens with the volume of the cells they inhabited; weight per unit volume ratios are consistently biased toward females; the mean value for wasps is 1.37, and for bees it is 1.33 (*80*). Either these wasps and bees allot more space (per unit provisions) for their sons than for their daughters or else development is more expensive in males.

For five species of wasps, Krombein (*32*) counted the number of caterpillars in a sample of cells that later gave rise to either female or male wasps. On the basis of these data we have calculated the relative number of caterpillars stored in a female cell compared to a male cell. For all five species, this direct measure of provisioning is almost identical to the measure of relative cell volume (*81*). This is consistent

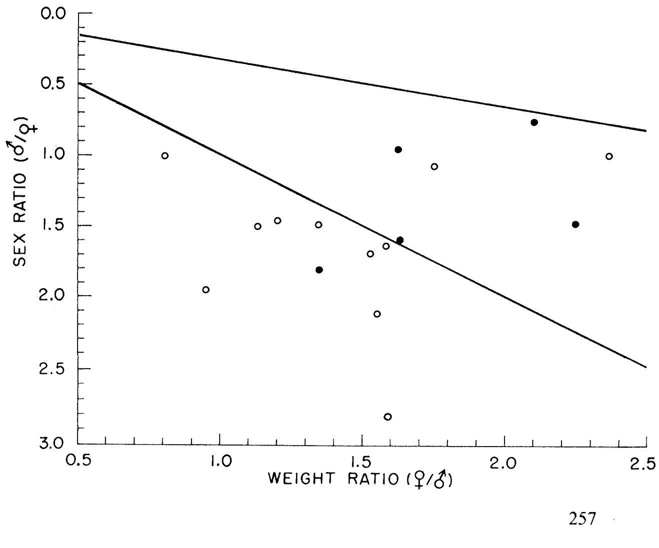


Fig. 6. The sex ratio as a function of the dry weight ratio for species of solitary bees (open circles) and solitary wasps (closed circles). Data are from natural nests (Table 4). The 1 : 1 and 1 : 3 lines are drawn as in Fig. 4.

with Krombein's impression that there was no average difference in the size of caterpillars stored in the two kinds of cells (*78*). To check this impression we weighed the contents of 24 cells of *Euodynerus foraminatus apopkensis*; these were cells whose wasps failed to develop but for which Krombein could reliably infer the sex of the intended wasp (*82*). For these 24 cells the mean relative weight of provisions (2.05) is very close to the mean relative cell volume (1.81) (*82*). These are virtually the only data available permitting a comparison of provisioning ratios with either cell volume ratios or adult weight ratios (*83, 84*). The only direct measure of developmental cost for any of the Hymenoptera suggests that development may indeed be more expensive in males; during pupation male ants (*Tetramorium*) lose about 30 percent of their caloric value while females, although similar in size, lose only about 15 percent of theirs (*35, 85*).

The sex ratio was plotted as a function of relative cell volume for 20 species of wasps (Fig. 7; data from Table 5). Although there is considerable scatter, the species are closer to a 1 : 1 ratio of investment than to a 1 : 3. The data are fitted by the linear regression

$$y = 1.1x - 0.34$$

There is a significant tendency ($P < .01$) for sex ratio and relative cost to be inversely related. The mean ratio of investment based on cell volume is 1.39 for wasps and 1.28 for bees. The ratio based on dry weight is 1.92 for wasps and 2.11 for bees. Similar data have been analyzed from the work of Danks (*86*) who combined data from natural nests with data from stems of plants made available to wasps and bees. The ratio of investment in these species approximates 1 : 1 (Fig. 8).

Taken together the available data from solitary bees and wasps support the expectation that ratios of investment in the solitary Hymenoptera are typically near 1 : 1 and no greater than 1 : 2. When an individual son is relatively less costly than an individual daughter, relatively more sons tend to be produced. Trap-nests should permit more precise measures of relative cost than presented here (*87*).

Ratio of Investment in Social Bees and Wasps

Like ants, eusocial bees and wasps are expected to show ratios of investment biased toward females. Since laying workers are known to be an important source of males in some species of bees and wasps (*10*), ratios of investment in social bees and wasps are not, in general, expected to be as biased toward females as in ants (Fig. 1). Unfortunately, it is much more difficult to ascertain the ratio of investment in social bees and wasps than in either ants or solitary bees and wasps. To tell workers from reproductives requires careful, time-consuming behavioral and morphological studies, and these yield too few sex ratio data for our purposes (*88*). In addition, since female reproductives are hard to distinguish from workers, it is difficult to get an accurate estimate of the relative cost of a reproductive female (compared to a male). We limit ourselves here to detailed data available for bumblebees (*Bombus*) and the closely related parasite (*Psithyrus*).

A temperate bumblebee colony survives

Table 5. The sex ratio (male/female), weight ratio (female/male), cell volume ratio (female/male), and weight per volume ratio (female/male) for the species of solitary wasps and bees studied by Krombein (*32*). The weight per volume ratio is based only on the cell volumes of those specimens that were weighed. By contrast the cell volume ratio is based on the cell dimensions of all individuals reared. The sex ratio and number of adults reared includes a few individuals whose sex was inferred (*75*). The species are presented in the order in which Krombein (*32*) presents them.

Superfamily, family, and species	Adults reared (No.)	Sex ratio	Cell volume ratio (F/M)	Weight-F (mg)	S.D.	Weight-M (mg)	S.D.	Weight ratio (F/M)	Weight per volume ratio
Vespoidea (wasps)									
Vespidae									
Monobia quadridens	227	0.89	1.39	68.2	10.5	35.4	11.8	1.93	1.52
Euodynerus foraminatus foraminatus	96	2.56	1.70	19.0[b]	3.4	12.8	3.4	1.49	1.01
E. f. apopkensis	1,551	2.30	1.69	22.9	2.6	11.0	3.0	2.07	1.33
E. megaera	240	0.67	1.74	28.2	2.9	12.9	2.0	2.22	1.28
Pachodynerus erynnis	240	0.71	0.91	28.0	7.2	12.6[b]	2.3	2.16	3.32
Ancistrocerus antilope antilope	375	1.88	1.48	30.1	4.3	15.8	1.5	1.90	2.0
A. campestris	83	1.77	1.62	18.9	3.6	9.0	2.3	2.10	1.15
A. catskill	189	0.97	1.39	15.5	2.9	6.8	1.2	2.28	1.38
A. tigris	114	0.27	1.53	11.9[b]	2.6	5.0[b]	0.9	2.37	1.85
Symmorphus cristatus	114	1.04	1.20	6.6[a]	0.64	3.4[b]	0.96	1.92	1.12
Stenodynerus krombeini	69	0.86	0.95	9.8	1.5	9.1	1.9	1.07	1.26
S. lineatifrons	92	0.46	0.63	10.5[b]	1.4	5.4[b]	1.4	1.95	1.95
S. saecularis	149	0.69	0.77	17.3[b]	3.8	12.5	2.1	1.39	1.25
S. toltecus	82	0.71	1.34						
Pompilidae									
Dipogon sayi	107	0.41	1.05	10.2[b]		3.0	0.67	3.46	3.46
Sphecidae									
Trypargilum tridentatum tridentatum	332	0.77	0.90	9.1	2.2	10.1	2.3	0.90	0.77
T. clavatum	314	0.89	1.00	11.8	2.0	7.9	1.3	1.50	1.01
T. johannis	72	1.18	1.38	17.3	3.8	13.8	1.8	1.26	0.82
T. striatum	349	1.60	1.80	24.7	4.1	19.0	3.9	1.30	1.03
Trypoxylon frigidum	82	0.71	1.16	2.0[b]	0.24	1.4	0.37	1.40	0.98
Apoidea (bees)									
Megachilidae									
Anthidium maculosum	78	0.3	1.0	34.4	3.6	37.0	6.4	0.93	2.38
Prochelostoma philadelphi	85	0.25		3.7[b]	0.38	3.3	1.0	1.11	1.14
Ashmeadiella meliloti	136	0.64	1.5	6.5	0.55	2.8	0.62	2.31	0.97
A. occipitalis	845	0.31	1.29	14.9[b]	3.6	7.1	2.6	2.10	1.29
Osmia lignaria lignaria	732	2.08	1.49	35.1	4.7	14.7	2.3	2.42	
O. pumila	315	0.38	1.24	9.4	1.6	5.1	1.6	1.84	1.23
Megachile gentilis	290	5.04	1.0	18.7	2.0	12.8	2.5	1.46	
M. mendica	208	2.71	1.0	33.2	6.8	16.7	3.3	1.99	

a = sample size of 2; b = sample size of 4.

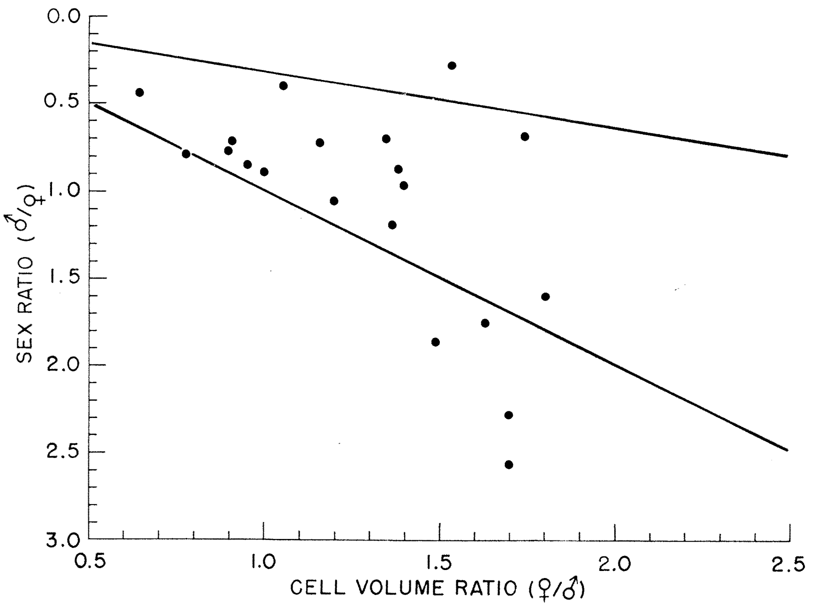
for only a season (*10*), the fertilized females overwintering alone. Reproductive females are produced in late summer at a time when few or no workers are being produced. Young queens remain on the nest for considerable periods where they are readily distinguished from workers. By marking emerging queens and males, Webb (*34, 89*) gathered extensive sex ratio data for five species of *Bombus* (and one parasite, *Psithyrus*). These data are presented in Table 6, along with mean weights of male and female reproductives. The sex ratios are all biased in favor of males, and this appears to be general in *Bombus* (*90*). Ratios of investment for the five species lie between 1 : 1.2 and 1 : 3.1.

Psithyrus variabilis is a parasite on *Bombus americanorum* (*34, 89*). A *Psithyrus* queen invades a *Bombus* nest, destroys the host larvae, and rears her own young using the food stores of her host and considerable help from the host workers (*34, 89*). If the *Psithyrus* queen is able to control the ratio of investment then one expects a 1 : 1 ratio and not the 1 : 2 ratio one observes (Table 6). Compared to ratios for the five species of *Bombus*, the ratio in *Psithyrus* is certainly not biased toward 1 : 1 (as expected), but it is difficult to compare the ratios directly, since mean *Psithyrus* female weight is based entirely on queens caught in the fall while each of the mean *Bombus* female weights is based largely on females caught in the spring after hibernation (and hence weight loss).

Evolution of Worker-Queen Conflict

The information we have reviewed forms an interesting pattern. In monogynous ants the queen appears to produce most or all of the males and the workers apparently control the rate of investment. Where our information is most reliable, this certainly appears to be true (for example, *Solenopsis invicta*, Table 2). The repeated evolution in ants (*5*) of trophic eggs (eggs produced to feed other ants) suggests that in some groups of ants male production by workers was formerly more important than it is now, the queen having regained control of male production and forced a new function on worker-laid eggs. The ant species with the greatest known worker contribution to male production is polygynous (*91*). In some monogynous social bees and wasps, workers contribute heavily to male production (*5, 6*). Why is the queen able to control male production in some species but not in others? Why in monogynous ants is she apparently powerless to affect the ratio of investment (Fig. 4A)? In answering these questions we outline here a theory for the evolution of worker-queen conflict.

1) *The asymmetry in aggressive encounters between queen and worker.* Aggressive encounters involve violence or the threat of violence. Where two combatants are related, each is expected to adjust its behav-



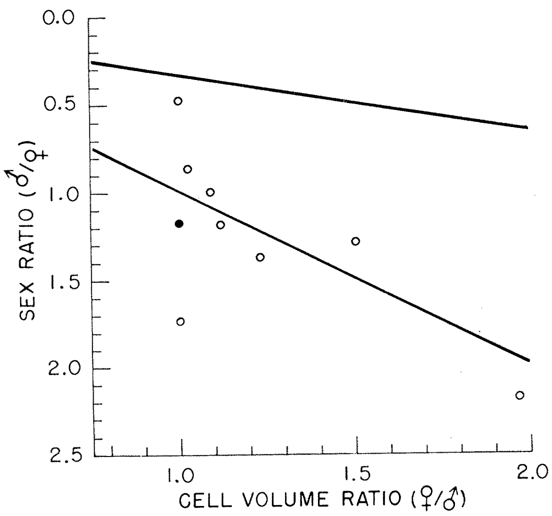


Fig. 7 (left). The sex ratio as a function of the cell volume ratio (female/male) for species of solitary wasps trap-nested by Krombein (*32*) (Table 5). Fig. 8 (right). The sex ratio as a function of the cell volume ratio for species of solitary wasps (open circles) and bees (closed circle). Natural nests and trap-nests combined by Danks (*86*).

Table 6. The ratio of investment in *Bombus* and its parasite, *Psithyrus*. The sex ratio data are from Webb (*34*). For *Bombus* the weights of females are based entirely on specimens caught in the spring, while *Psithyrus* females were all caught in the fall (before hibernation).

Species	Reproductives counted (No.)	Colonies (No.)	Sex ratio	Weight-F (mg)	S.D.	Weight-M (mg)	S.D.	Weight ratio (F/M)	Ratio of investment
				Species of Bombus					
B. americanorum	1780	25	1.52	274.9^{c}	32.0	82.4	27.4	4.17	1 : 2.74
B. auricomus	302	12	1.14	330.3^{a}	10.2	136.3	22.8	2.42	1 : 2.12
B. fraternus	268	4	1.34	315.2^{b}	95.28	195.1	32.6	1.62	1 : 1.21
B. griseocollis	887	20	1.72	207.3^{b}	27.1	102.4	8.9	2.02	1 : 1.17
B. impatiens	351	5	1.42	234.8^{d}	106.9	54.9	20.2	4.44	1 : 3.13
				Species of Psithyrus					
P. variabilis	290	4	0.91	164.8^{a}	29.0	79.9	19.6	2.06	1 : 2.06

The mean weight for males is based on a sample size of five individuals. For females: a = 2 individuals; b = 3; c = 4; d = 6.

ior according to the possibility of lowering its inclusive fitness by harming a relative (*92*). In a conflict between a queen and a laying worker, there is an important asymmetry in the way in which each individual is expected to view the possibility of damaging the other. To take the extreme case, early in the life of a large, perennial monogynous ant colony the queen could kill a daughter and we would barely be able to measure the resulting decrease in either party's inclusive fitness. By contrast, a worker who kills her mother harms her own inclusive fitness in three different ways. She destroys the one highly specialized egg layer in the colony. She destroys the one individual capable of producing reproductive females to whom the worker is related by 3/4. And she destroys the one individual capable of producing new workers (and hence keeping the colony alive). In short, the worker inflicts a catastrophic loss on her own inclusive fitness.

In such situations there is a large bias in favor of the queen winning any aggressive encounter with her workers. The bias in favor of the queen is largest where the colony is expected to reproduce again in the future (perennial colonies), where there is no alternate, closely related reproductive to whom the workers can attach themselves (for example, monogynous ants), where the queen is strongly specialized as an egg layer, and where the ratio of investment is controlled by the queen (since this decreases the expected RS of the males produced when the queen is destroyed, assuming only males can still be produced). Aggression, as we shall see, is expected to have an important influence on male production but little or none on the ratio of investment.

2) *The relevance of aggression to the production of males.* Within a colony a small number of acts result in the laying of the male-producing eggs for a season. If the queen can be present, at or soon after these events, then her advantage in aggressive encounters should permit her to destroy worker-laid eggs, provided that she can recognize such eggs. Alternatively, if she can detect other potential egg layers, she may be able to attack them directly. To discriminate worker-laid eggs from her own, the queen must see them being laid, find them in places or circumstances where her own eggs are not, or learn to discriminate the two kinds of eggs. There is evidence for all three kinds of discrimination (*5, 10, 34, 93*). In particular, Gervet (*93*) has shown that *Polistes* females antennate the first several eggs they lay and may eat one or two. When deprived of this experience, a female does not develop the capacity to discriminate strange eggs from her own. Regardless of experience, the female does not destroy eggs that are more than 3 hours old. In short, the mechanisms are known by which a queen can easily discriminate against many worker-laid eggs. In addition, it is difficult to see how a worker could become an effective laying worker yet conceal this fact from the queen. West Eberhard (*34*) has suggested that in *Polistes* a female will fail to destroy an egg if she does not have one herself to lay, so that both the capacity to produce male eggs and to destroy those of the queen must depend on how often a laying worker is fed (and how rarely she feeds others). This, in turn, ought to depend on how attractive such an individual is to other workers or how aggressively she begs from them (without herself being altruistic). Queens should be selected to be aggressive toward workers attractive to others and to be aggressive toward begging workers who are themselves not altruistic. In summary, deception cannot save either the laying worker or most of her eggs.

3) *Annual versus perennial colonies.* In an annual bumblebee colony, killing the queen at the time when male eggs are being laid should not in itself lower the eventual output of the colony by much because, once male production begins, no more workers are produced anyway, and the colony does not survive beyond the production of reproductives. Of course if workers are unfertilized, the entire production of the altered colony must consist of males; but if workers control the ratio of investment then the males' expected RS must equal that of a similar mass of females, so that initially there is only a slight selection pressure against killing the queen. However, it cannot be assumed that the total production of the altered colony will equal that of the colony with the queen intact, for more conflict is expected in the altered colony (*94*), especially if it is large and no one individual can dominate all others. In summary, worker production of males is much more likely in annual colonies than during most of the life of perennial colonies, but there still remains some bias in favor of the queen.

It is noteworthy that worker-queen conflict and reciprocal egg-eating have been known in the annual colonies of bumblebees since the 19th century, but male production is only known to occur largely by laying workers in one species, *Bombus atratus*, which is perennial. According to our theory, male production by the queen in ants is associated with the perennial colonies typical of this group.

4) *The relationship between polygyny and laying workers.* If workers easily lose in fights with their mother because of her unique reproductive role, then polygynous societies where the several queens are close relatives should be characterized by workers who are much more willing to risk injuring their mother than workers in monogynous colonies are (*95*). Although it would be preferable to gain one's way without harming one's mother, injuring her is associated with less drastic effects on the workers' inclusive fitness since they can at least transfer their work to close relatives. We thus predict that polygyny should be associated with laying workers. Arguing from a hypothesized association between inbreeding and polygyny, Hamilton (*6*) came to the opposite conclusion (*96*); but he admitted that the only available evidence shows an association between being polygynous and having laying workers produce many of the males (*91*).

5) *Conflict over the ratio of investment.* Laying the male-producing eggs can be achieved by a small number of acts, but the ratio of investment (which includes all that goes into rearing the reproductives) results from thousands upon thousands of acts. In addition, the queen—via egg destruction—can often aggressively dominate male production, but it is much more difficult aggressively to impose a ratio of investment. By laying more male eggs than the workers would prefer, the queen may begin with a sex ratio that would, without intervention, lead to equal investment. But the workers care for the eggs and with care goes the power to destroy. The queen may guard her male eggs, but once they hatch they will need care from workers (*97*). As the larvae grow, execution of excess males becomes increasingly inefficient and underfeeding more likely. Consistent with this argument is the discovery that adult male ants lose weight while their reproductive sisters are being fattened up (*35*).

If workers can evolve the ability to estimate the ratio of investment within their colony, then they will be able to counteract the queen's maneuvers more efficiently and more precisely. In other words, the capacity to measure and produce a given ratio of investment (which may involve coordinating the activities of millions of workers) must lie within the workers. Perhaps the special cognitive strains of being a haplodiploid worker account in part for the enlargement of the brain in the social Hymenoptera in contrast to its diminution in the termites (*6*).

6) *The concept of offspring power.* The data that we have gathered are inconsistent with the notion of complete parental domination (*13*). The female daughters of monogynous ant queens appear to completely dominate their mothers where the ratio of investment is concerned, while she enjoys in the same species nearly complete domination of the genetics of male production. The queen's royal status (highly pro-

tected, completely cared for, and the recipient of much altruism and deference) flows from her unique genetic role, but this role does not give her royal powers—at least not where care for her offspring is concerned (the ratio of investment). Instead, the relevant principle is more like: to those who do the work shall be delegated the authority over how such work is allocated. But our slave-making data show that this cannot be a general principle. Likewise, we have no data that would show whether the reproductives in the system get more investment than either the queen or her working daughters prefer. However, Brian has made the remarkable discovery that workers in *Myrmica rubra* have to actively bite larvae in order to decrease the number that develop into reproductives (*98*), and this is reminiscent of the inefficiencies of weaning conflict in mammals. Instead of supporting a general principle predicting who shall dominate situations of conflict, our work supports the notion that there is no inherent tendency for evolution to favor any particular party in situations of conflict.

Summary

Hamilton (*1*) was apparently the first to appreciate that the synthesis of Mendelian genetics with Darwin's theory of natural selection had profound implications for social theory. In particular, insofar as almost all social behavior is either selfish or altruistic (or has such effects), genetical reasoning suggests that an individual's social behavior should be adjusted to his or her degree of relatedness, *r*, to all individuals affected by the behavior. We call this theory kinship theory.

The social insects provide a critical test of Hamilton's kinship theory. When such theory is combined with the sex ratio theory of Fisher (*9*), a body of consistent predictions emerges regarding the haplodiploid Hymenoptera. The evolution of female workers helping their mother reproduce is more likely in the Hymenoptera than in diploid groups, provided that such workers lay some of the male-producing eggs or bias the ratio of investment toward reproductive females. Once eusocial colonies appear, certain biases by sex in these colonies are expected to evolve. In general, but especially in eusocial ants, the ratio of investment should be biased in favor of females, and in ants it is expected to equilibrate at 1 : 3 (male to female). We present evidence from 20 species that the ratio of investment in monogynous ants is, indeed, about 1 : 3, and we subject this discovery to a series of tests. As expected, the slave-making ants produce a ratio of investment of 1 : 1, polygynous ants produce many more males than expected on the basis of relative dry weight alone, solitary bees and wasps produce a ratio of investment near 1 : 1 (and no greater than 1 : 2), and the social bumblebees produce ratios of investment between 1 : 1 and 1 : 3. In addition, sex ratios in monogynous ants and in trap-nested wasps are, as predicted by Fisher, inversely related to the relative cost in these species of producing a male instead of a female. Taken together, these data provide quantitative evidence in support of kinship theory, sex ratio theory, the assumption that the offspring is capable of acting counter to its parents' best interests, and the supposition that haplodiploidy has played a unique role in the evolution of the social insects.

Finally, we outline a theory for the evolution of worker-queen conflict, a theory which explains the queen's advantage in competition over male-producing workers and the workers' advantage regarding the ratio of investment. The theory uses the asymmetries of haplodiploidy to explain how the evolved outcome of parent-offspring conflict in the social Hymenoptera is expected to be a function of certain social and life history parameters.

References and Notes

W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964); J. B. S. Haldane, *Nature (London) New Biol.* **18**, 34 (1955); G. C. Williams and D. C. Williams, *Evolution* **11**, 32 (1957).

2. J. Maynard Smith and M. G. Ridpath, *Am. Nat.* **106**, 447 (1972).

G. E. Woolfenden, *Auk* **92**, 1 (1975); I. C. R. Rowley, *Emu* **64**, 251 (1965).

4. E. O. Wilson, *Sociobiology* (Harvard Univ. Press, Cambridge, Mass., 1975).
5. ______, *The Insect Societies* (Harvard Univ. Press, Cambridge, Mass., 1971).
6. W. D. Hamilton, *Annu. Rev. Ecol. Syst.* **3**, 193 (1972).
7. R. L. Trivers, in *Sexual Selection and the Descent of Man 1871–1971*, B. Campbell, Ed. (Aldine, Chicago, 1972), pp. 136–179.

______, *Am. Zool.* **14**, 249 (1974).

9. R. A. Fisher, *The Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930). In diploid organisms (in the absence of inbreeding), natural selection favors equal investment in the two sexes. Where investment in a typical male produced equals investment in a typical female, natural selection favors the production of a 50 : 50 sex ratio—regardless of differential mortality by sex after the period of parental investment. For a definition of parental investment, see Trivers (*7*). For preferred sex ratios under inbreeding, see W. D. Hamilton, *Science* **156**, 477 (1967). In the absence of inbreeding, Fisher's argument applies to haplodiploid species. For the effects of inbreeding on the parents' preferred sex ratio in haplodiploid species, see Hamilton (*6*). Hamilton's argument on this point must be modified for species with laying workers, as pointed out to us by J. Pickering, Harvard Biology Department. For the offspring's preferred sex ratio (and the male parent's) in typical diploid species, see Trivers (*8*).
10. C. D. Michener, *The Social Behavior of the Bees* (Harvard Univ. Press, Cambridge, Mass., 1974).
11. Slightly more precise formulations are found in Hamilton (*6*). Under inbreeding, *r* must be redefined to take into account the probability that an individual will have two copies of an allele that is identical by descent.
12. Several of the degrees of relatedness in Hamilton (*1*) and Wilson (*5*) are in error. For corrections, see W. D. Hamilton, in *Group Selection*, G. C. Williams, Ed. (Aldine, Chicago, 1971); R. H. Crozier, *Am. Nat.* **104**, 216 (1970); and (*6*).
13. By contrast, R. D. Alexander [*Annu. Rev. Ecol. Syst.* **5**, 325 (1974)] has argued that offspring should naturally act in their parents' best interests, but, in our opinion, neither the arguments presented nor the evidence available support this viewpoint. For example, the spread of alleles conferring selfish behavior on offspring may reduce the eventual reproductive success of both parent and offspring but this is not an argument against the spread of such alleles (although it is an argument for choosing a mate who was selfless when young). Similarly, the ability of the parent to respond to offspring selfishness by harsh retaliation is limited by the parent's growing investment in an offspring, as well as by the offspring's growing independence of the parent (*8*). Alexander interprets the apparent conflict in parent-offspring relations as an efficient system by which the two parties communicate regarding the optimal parental strategy, but this view fails to answer three questions (*6, 8*): (i) Why is such a system of communication not vulnerable to the kinds of deceit already described for vertebrates and social insects? (ii) In what way are kicking, biting, and screaming, or reciprocal egg-eating, efficient systems of communication? (iii) And finally, if conflict occurs because of different estimates of the same parameters, why are parent and offspring estimates predictably biased in favor of the estimator? Total parental domination has also been argued by M. T. Ghiselin, *The Economy of Nature and the Evolution of Sex* (Univ. of California Press, Berkeley, 1974). See also R. L. Trivers, *Science* **186**, 525 (1974); W. D. Hamilton, *Q. Rev. Biol.* **50**, 175 (1975). For an introduction to kinship theory M. J. West Eberhard, *ibid.*, p. 1.
14. C. D. Michener, *Annu. Rev. Entomol.* **14**, 299 (1969). For a review of the literature on the social insects, see Wilson (*5*). For a discussion of the important "primitively eusocial" bees, see Michener (*10*).
15. This point was first brought to our attention by D. M. Windsor of the Smithsonian Tropical Research Institute. Windsor independently derived many of our conclusions.
16. Because a male typically invests nothing in the offspring, his only avenue to a biased sex ratio of investment is through his sperm. These are selected to wriggle through to fatherhood more often than the potential mother would prefer, thereby selecting for a spermatotheca under subtle sphinctral control. Since any success of such sperm automatically raises the value to mothers of producing sons, it is difficult to imagine how spermal ingenuity could compete with motherpower for long.
17. This assumes that such species are typically outbred and that queens are actually or effectively singly inseminated (as when sperm of successive fathers are highly clumped). All full sisters agree among themselves on the preferred ratio of investment, so that the mother's power is pitted against that of a united three-fourths sisterhood.
18. J. Pickering, personal communication.
19. It is desirable to solve the equation $r_M \times$ the expected $RS_M = r_F \times$ the expected RS_F, where r_M is the *r* of an interested party (workers) to reproductive males and the expected RS_M is the expected RS of a male (per unit effort), measured by both the number of females he is expected to inseminate and by his average *r* to his mates' offspring. From the nonlaying workers' standpoint (where *x* is the ratio of investment in males compared to females) the equation reads
$$\left(\frac{3-p}{8}\right)\left(1 + \frac{1-p}{2}\right) = \frac{3x}{4}\left(\frac{1}{2} + \frac{1+p}{4}\right)$$
20. See G. C. Williams, *Sex and Evolution* (Princeton Univ. Press, Princeton, N. J., 1975). Inbreeding also decreases heterozygosity. The large degree of genetic variability that is found within sexual species supports Williams' arguments as well as the claim that inbreeding is usually trivial. For further evidence, see R. C. Lewontin, *The Genetic Basis of Evolutionary Change* (Columbia Univ. Press, New York, 1974).
21. A. F. Skutch, *Condor* **63**, 198 (19 J. L. Brown, *Am. Zool.* **14**, 63 (1974).
22. C. J. Ralph and C. A. Pearson, *Condor* **73**, 77 (1971).
23. G. B. Schaller, *The Serengeti Lion* (Univ. of Chicago Press, Chicago, 1972).
24. L. D. Mech, *The Wolf* (Natural History Press, New York, 1970); J. Van Lawick-Goodall and H. Van Lawick, *Innocent Killers* (Houghton Mifflin, Boston, 1971).
25. Selection would not necessarily favor the production of a male capable of fertilizing all of a queen's daughters, because the cost of such a male to those that produce him may outweigh his benefits to them.
26. G. A. Parker, *Biol. Rev. Cambridge Philos. Soc.* **45**, 525 (1970); S. Taber, *J. Econ. Entomol.* **48**, 552 (1955).
27. A male's *r* to reproductives that he might help

rear (his siblings) will also change as a function of p, as will a female's; but the difference between the two is slight, especially if there is more than one laying worker per nest. When only one laying worker produces all of the males in each nest, a male is more related (than is a female) to other reproductives in the nest by a factor of 10 : 9. (With additional laying workers, this factor approaches 1.0.) In general, with a single laying worker per nest the average r of a male to reproductives divided by the average r of a female to reproductives is

$$2\,(2p^2 - 3p + 5)\;/\;(9 - p)$$

This value varies between 1.11 and 0.93.

28. B. Hölldobler, personal communication.
29. ———, *Z. Angew. Entomol.* **49**, 337 (1962).
30. ———, *Z. Vgl. Physiol.* **52**, 430 (1966). Males apparently feed each other more often than they feed reproductive females or workers (*28*), and this bias is exactly consistent with the greater expected RS of males assuming workers are able to bias the ratio of investment or lay some of the male-producing eggs (Fig. 3). Hamilton (*6*) is apparently mistaken in supposing that *Camponotus* tend to inbreed (*29*).
31. R. L. Jeanne, *Bull. Mus. Comp. Zool. Harv. Univ.* **144**, 63 (1972).
32. K. Krombein, *Trap-nesting Wasps and Bees: Life Histories, Nests and Associates* (Smithsonian Press, Washington, D.C., 1967).
33. D. J. Peckham, F. E. Kurczewski, D. B. Peckham, *Ann. Entomol. Soc. Am.* **66**, 647 (1973); R. M. Bohart and P. M. Marsh, *Pan-Pac. Entomol.* **36**, 115 (1960); C. G. Hartman, *Entomol. News* **55**, 7 (1944); M. N. Paetzel, *Pan-Pac. Entomol.* **49**, 26 (1973). For *Trypargilum*, see also Krombein (*32*).
34. M. J. West Eberhard, *Misc. Publ. Mus. Zool. Univ. Mich. 140* (1969); M. C. Webb III, thesis, University of Nebraska (1961). Alternatively, as both authors suggest, the workers may be guarding against inbreeding.
35. G. J. Peakin, *Ekol. Pol.* **20**, 55 (1972).
36. A. Buschinger, *Insectes Soc.* **15**, 89 (1968).
37. ———, *Zool. Anz.* **186**, 242 (1971); C. P. Haskins and R. M. Whelden, *Psyche* **72**, 87 (1965). Thus, there is no inherent block to sexual reproduction by workers.
38. Reviewed in S. F. Sakagami and K. Hayashida, *J. Fac. Sci. Hokkaido Univ. Ser. VI Zool.* **16**, 413 (1968). Comparison of 12 primitively eusocial bees reveals no correlation between the percentage of workers with ovarial development and the percentage of workers that are inseminated. Within *Lasioglossum duplex* at least, there is a weak tendency for inseminated females to show some ovarial development. Insemination of workers may be useful if the queen weakens or dies.
39. Each of the subgenera of primitively eusocial bees reviewed by Michener (*10*) shows some or all of these trends, but quantitative data are still too weak to permit detailed correlations between numbers of males produced, degree of worker insemination, and frequency of worker supersedure.
40. C. R. Watts and A. W. Stokes, *Sci. Am.* **224**, 112 (June 1971).
41. For example, in *Aphaenogaster rudis* workers are capable of producing males when the queen is dead, but when she is alive she apparently produces most or all of the males [R. H. Crozier, *Isozyme Bull.* **7**, 18 (1974)].
42. This is true for *Leptothorax curvispinosus, L. duloticus*, and *Prenolepis imparis* (data separated by M. Talbot).
43. For one monogynous species (*Camponotus herculeanus*) we used data on alates counted while leaving the nest. For another species (*Tetramorium caespitum*), reproductives were removed from the nests each year, leaving the nests intact so that they could be sampled in succeeding years (each year's sampling of a given nest is counted as a separate nest).
44. There is strong variance between nests in the sex ratio produced. Small nests within some species apparently tend to produce males (*35*). Producing one sex at a time may be a ploy to reduce male selfishness, assuming that males are sensitive to the sex ratio of reproductives within a nest (since they will typically value other males more than female reproductives).
45. Relative dry weight was chosen (instead of relative wet weight), on the assumption that water is relatively inexpensive to an ant colony. For several species, the dry weights were found by collecting live alates, killing, drying, and weighing them. (Alates were dried for 1 hour at 275°F; additional drying had no effect on dry weight.) For most of the rest of the species, we weighed dried specimens in the collection of the Museum of Comparative Zoology (Harvard), and we normally weighed five individuals of each sex. For five species (Table 2), specimens preserved in alcohol were dried and weighed. Although two authorities on ants guessed that females would lose relatively more weight while being dried, the reverse was invariably true: males commonly lose about two-thirds of their weight, while females lose somewhat less than half of theirs. Thus the wet weight ratio is larger than the dry weight ratio by a mean factor of 1 : 1.7 (geometric mean for seven species; range, 1.4 to 1.9). Since it is unlikely that water has no cost to the colony, the true relative cost may lie between the dry weight ratio and the wet weight ratio but closer to the dry weight ratio.
46. A number of methodological safeguards were used. All sex ratio data were gathered in ignorance of the relative cost of the two sexes. For each species weighed, H.H. weighed male and female specimens (usually singly) on a Mettler balance scale, type B6 (precision to ± 0.01 mg). Whenever we chose specimens to weigh from a larger sample, they were chosen without knowledge of the relevant sex ratio. More than half of the specimens weighed were sent to us by other scientists in response to our request for five specimens of each sex that were typical by size. None of the scientists knew of the predictions being tested.
47. In our opinion the six monogynous species with the best data are *Formica pallidefulva, Leptothorax curvispinosus, Myrmica sulcinodis, Prenolepis imparis, Solenopsis invicta*, and *Tetramorium caespitum*.
48. Bomb calorimetry was performed for us by the Warf Institute (Madison, Wis.) with an estimated accuracy of ± 10 percent. Each female sample was slightly higher in calories per gram than the comparable male sample. Two species of *Camponotus*: male, 4.8 kcal/g, female (incomplete burns), 5.15 kcal/g. Composite males of *Myrmica emeryana, Aphaenogaster rudis*, and *Pogonomyrmex barbatus*, 5.16 kcal/g. Female *Myrmica emeryana*, 5.19 kcal/g, *Aphaenogaster rudis* (incomplete burns), 6.62 kcal/g, and *Pogonomyrmex barbatus*, 6.29 kcal/g.
49. R. G. Wiegert and D. C. Coleman, *BioScience* **20**, 663 (1970).
50. W. L. Morrill, *Environ. Entomol.* **3**, 265 (1974); personal communication; G. P. Markin and J. H. Dillier, *Ann. Entomol. Soc. Am.* **64**, 562 (1971).
51. M. V. Brian, *Ekol. Pol.* **20**, 43 (1972).
52. L. Passera, personal communication.
53. This prediction should also hold for parasitic ants (*5*) except that such species are likely to practice adelphogamy, resulting in a strong bias toward females (*6, 9*). Ratios of investment in parasitic ants do appear to be biased toward females (*6*). *Sifolinia laurae* females are larger than males and more numerous (*51*). The same is true of *Plagiolepis xene* (*52*). As is consistent with the hypothesis of adelphogamy, nearly every nest of *P. xene* that was examined by Passera (8 of 11) produced at least one or two males.
54. As in *Leptothorax curvispinosus*, nests consisted of individual acorns and other nesting places in which *Leptothorax duloticus* were found. For additional information on *L. duloticus*, see M. Talbot, *Ecology* **38**, 449 (1957); L. G. Wesson, *Bull. Brooklyn Entomol. Soc.* **35**, 73 (1940); E. O. Wilson, *Evolution* **29**, 108 (1975).
55. A. Buschinger, personal communication. Buschinger sent us specimens stored in alcohol which we dried and weighed. For additional information on the biology of the species, see A. Buschinger, *Insectes Soc.* **13**, 5 (1966); *ibid.*, p. 311; *Zool. Anz.* **187**, 184 (1971).
56. M. Talbot, unpublished data gathered at the E. S. George Reserve, Pinckney, Mich. All specimens were sent in alcohol by Talbot and dried and weighed by us.
57. A. E. Headley, *Ann. Entomol. Soc. Am.* **36**, 743 (1943) (10 nests); M. Talbot (*56*) (72 nests). For additional observations on the species, see E. O. Wilson, *Ann. Entomol. Soc. Am.* **67**, 777 (1974); *ibid.*, p. 781.
58. The dry weight of the slave-making queen may be reduced because she founds a colony by expropriating a nest of the slave species; hence she may need little in fat reserves.
59. In nests of both *Leptothorax duloticus* and *Harpagoxenus sublaevis* the slaves greatly outnumber the slave-makers (*36, 55, 56*). The slaves gather all of the food and do all of the nest and brood care.
60. D. H. Janzen, *J. Anim. Ecol.* **42**, 727 (1973).
61. Polygynous nests, usually temporary, may also arise when young queens (perhaps sisters) work together to found a new colony [C. Baroni-Urbani, *Zool. Anz.* **181**, 269 (1968)]. Queens and workers are not expected to agree on relative merits of monogyny and polygyny. Workers are more likely to favor a reproductive sister joining the nest than is the queen, and in at least one ant species, *Camponotus herculeanus*, polygynous queens are tolerated by workers but act aggressively among themselves (*29*). By contrast, two related females are more likely to agree to continue the polygyny, and polygyny between founding females often ends when the first workers eclose [N. Waloff, *Insectes Soc.* **4**, 391 (1957)]. For detailed studies of any polygyny, see A. Buschinger, thesis, Würzburg University (1967).
62. Inclusion of reproductive daughters in the nest also changes the average r between workers and the male and female reproductives that they finally rear. Insofar as workers are rearing the offspring of someone other than their mother, they will tend to prefer a 1 : 1 ratio of investment.
63. This is a general argument. In any species in which the offspring of one sex, after the end of the period of parental investment, inflict a cost on their parents not inflicted by offspring of the opposite sex, then the inflicting sex will be produced in smaller numbers than expected on the basis of parental investment. The argument holds in reverse for altruistic behavior performed by offspring of one sex. This suggests a simple way to measure whether helpers at the nest (for example, in birds) are really helping or are inflicting a net cost on their parents [A. Zahavi, *Ibis* **116**, 84 (1974); J. Brown, *ibid.* **117**, 243 (1975)], or are helping only enough to make up for costs they are inflicting. The sex ratio that is produced should show appropriate biases. This argument may explain some of the sex ratio variation in bird species with helpers.
64. The following polygynous *Formica* appear to have male-biased ratios of investment: *F. obscuriventris* [M. Talbot, *Anim. Behav.* **12**, 154 (1964)]; *F. ulkei* and *F. obscuri* [———, *Am. Midl. Nat.* **61**, 124 (1959)]; *F. opaciventris* [G. Scherba, *J. N.Y. Entomol. Soc.* **69**, 71 (1961)]. See also M. Ito and S. Imamura, *J. Fac. Sci. Hokkaido Univ. Ser. VI Zool.* **19**, 681 (1974). Relative dry weight (F/M) in *Formica* is typically lower than 2 : 1.
65. D. H. Janzen, *Science* **188**, 936 (1975). The ratio of investment was based on a single nest for each species.
66. G. W. Elmes, personal communication: 21 nests were monogynous (2130 reproductives), four were polygynous (293 reproductives). Polygynous queens were microgynes (average, eight to a nest).
67. W. A. Sands, personal communication.
68. *Neotermes connexus* (sex ratio 2791 : 912; 55 nests were examined): H. A. Bess, in *Biology of Termites*, K. Krishna and F. M. Weesner, Eds. (Academic Press, New York, 1970), vol. 2. We have been unable to get specimens to weigh, but it is unlikely that females are more than 1.5 times as heavy as males (*67*).
69. M. L. Roonwal and S. C. Verma, *Ann. Arid Zone* **12**, 107 (1973); M. L. Roonwal and N. S. Rathore, *ibid.* **11**, 92 (1972). For one species, *Microcerotermes raja*, the dry weight ratio was calculated from Roonwal and Verma's linear measurements of the alates. A termite swarm consists of individuals who are just departing their nest.
70. W. A. Sands, *Insectes Soc.* **12**, 117 (1965). We thank W. A. Sands and M. T. Pearce of the Centre for Overseas Pest Research, London, England, for the use of their unpublished data on *Trinervitermes*. Specimens stored in ethanol were weighed after being dried for 1 minute on filter paper. For the five species of *Trinervitermes*, the sex ratios and the dry weight ratios are as follows.

	Sex ratio	Weight ratio
T. trinervius	61 : 136	1.15
T. germinatus	230 : 347	1.25
T. togoensis	60 : 101	1.18
T. oeconomus	95 : 114	1.27
T. occidentalis	52 : 214	1.18

Although the sex ratio data are sparse they are consistent with other indications of a female-biased sex ratio. For nomenclatural changes, see W. A. Sands, *Bull. Br. Mus. (Nat. Hist.) Entomol. Suppl. 4* (1965).

71. S. D. Jayakar and H. Spurway, *J. Bombay Nat. Hist. Soc.* **61**, 662 (1964).
72. Data from the following studies are likely to be biased in this fashion: K. A. Stockhammer, *J. Kans. Entomol. Soc.* **39**, 157 (1966); R. P. Kapil and S. Kumar, *J. Res. Punjab Agric. Univ.* **6**, 359 (1969); C. D. Michener, W. B. Kerfoot, W. Ramírez, *J. Kans. Entomol. Soc.* **39**, 245 (1966).
73. The depth of the holes available may also affect the sex ratio produced, as in *Megachile rotundata* [H. S. Gerber and E. C. Klostermeyer, *Science* **167**, 82 (1970)].
74. There is usually considerably greater mortality in trap-nests than in nature. If the mortality is differential by sex, then the sex ratio of adults when eclosing misrepresents the sex ratio at the time of parental investment (when the eggs were laid). In

general, species with little or no male parental investment (such as bees and wasps) are expected to show differential male mortality (*7*).

75. Plus *Stenodynerus krombeini* ($N = 69$). For some species, Krombein (*32*) was able to infer sex for some of the individuals who failed to develop and for these species the sex ratio we have used is based on all individuals reared plus those whose sex was inferred. Inclusion of individuals whose sex was inferred has only a slight (and nonsystematic) effect on the sex ratio measured.
76. All individuals were reared by Krombein (*32*) in trap-nests and were killed and pinned shortly after eclosing.
77. Weighted equally by the two dimensions, cell length and cross-sectional area.
78. K. V. Krombein, personal communication.
79. Also relevant to relative cost are features such as cell position and hence time of parental investment, cell partition width, and associated intercallary cells. Neither partition width nor associated intercallary cells appear to differ strikingly by sex (*32*), but female cells are often deeper in the nests; that is, they are the first to be occupied and the last to be vacated. The effect of these factors on relative cost is not clear.
80. This is also true for a larger sample (15 individuals of each sex) of *Euodynerus foraminatus apopkensis* (Table 5). Cell dimensions were not available for many of the specimens on which mean weights were based, thus Krombein picked out additional specimens to permit the measure of weight per unit volume.
81. For the five species, the provisioning ratio (sample size given in parentheses) and the cell volume ratio are: *Monobia quadridens* 1.38 (9), 1.39; *Euodynerus foraminatus apopkensis* 1.75 (77), 1.69; *E. megaera* 1.76 (9), 1.74; *E. schwarzi* 2.29 (11), 2.37; and *Ancistrocerus antilope* 1.21 (17), 1.48.
82. The caterpillars were removed from alcohol and dried for 18 hours before being weighed. Because the contents of some cells were lumped, it is not possible to calculate variances in the measures. Sample size: 8 females, 14 males, and 2 uncertain individuals that are likely to be males. For the same species (sample of 2 males and 2 females) the weight ratio of provisions (1.41) is very near the volume ratio of provisions (1.44) [J. T. Medler, *Ann. Entomol. Soc. Am.* **57**, 56 (1964)].
83. E. White, *J. Anim. Ecol.* **31**, 317 (1962). The weight ratio is based on White's data.
84. In *Osmia rufa* the provisioning ratio (1.3), based on the number of provisioning trips required to fill up two male cells and two female cells, was the same as the volume ratio (1.3), but not the same as the adult weight ratio (for all individuals, 1.7). The sex ratio was 1.4 [A. Raw, *Trans. R. Entomol. Soc. London* **124**, 213 (1972)]. In *O. lignaria* the peak larval weight ratio (1.4) is the same as the weight ratio of provisions consumed [M. D. Levin, *J. Kans. Entomol. Soc.* **39**, 524 (1966)]. In *Sphecius spheciosus* the adult weight ratio (2.4) is almost identical to the provisioning weight ratio (2.3) but the latter was only estimated [R. Dow, *Ann. Entomol. Soc. Am.* **35**, 310 (1942)]. In *Sceliphron spirifex* (*83*) the provisioning ratio is about 1.6 while male and female cell volumes are nearly identical, but this species is a mud dauber and does not build cells end to end in a limited space.
85. In *Megachile rotundata* the dry weight ratio for adults is only slightly greater (3 to 8 percent) than the wet weight ratio of larvae for three independent samples (*73*).
86. H. V. Danks, *Trans. R. Entomol. Soc. London* **122**, 323 (1971). Relative cell volumes are based on relative cell length alone since this is the only cell dimension that Danks supplies. For one of his species (*Cemonus lethifer*) Danks also provides weights of prepupae. The prepupal weight ratio ($N = 252$) is 1.29, slightly greater than the cell volume ratio (1.12).
87. In particular, prey that is stored must be weighed as well as counted. In addition, by watching females provision cells, one can measure the time spent in provisioning cells of different sizes.
88. For example, Jeanne (*31*) and West Eberhard (*34*) give sex ratio limited by small samples. C. D. Michener [*Bull. Am. Mus. Nat. His.* **145**, 221 (1971)] gives detailed sex ratio data for allodapine bees but it is very difficult to separate workers from reproductives in these bees. For other data, see Michener (*10*).
89. Since males leave the nest before young queens do, Webb's data probably slightly underestimate the number of males produced.
90. J. B. Free and C. G. Butler [*Bumblebees* (Collins, London, 1959)] give an estimate of 2 : 1 for the sex ratio in *Bombus* generally.
91. *Myrmica rubra* (Table 3) [M. V. Brian, *Insectes Soc.* **16**, 249 (1969)].
92. W. D. Hamilton, in *Man and Beast: Comparative Social Behavior* (Smithsonian Press, Washington, D.C., 1971). For the expected effects on aggressive behavior of asymmetries in the payoffs, see G. A. Parker, *J. Theor. Biol.* **47**, 223 (1974).
93. J. Gervet, *Insectes Soc.* **9**, 343 (1964).
94. Conflict is expected because each worker would prefer to produce sons rather than nephews. This conflict is also expected when the queen is alive, but workers then agree on the production of sisters which is the major part of their work.
95. The acacia trees that are host to ant colonies of *Pseudomyrmex* show a similar bias. Queens of monogynous species are protected within heavily fortified thorns, while queens of polygynous species occupy less protected ones (*60*).
96. For species such as *Myrmica rubra* polygyny apparently results when fertilized daughters are permitted to return to the colony of their origin. It is not known whether such females mate with close relatives. That inbreeding should be associated with laying workers is not a strong argument. Queens will be less antagonistic toward eggs laid by workers, but there will also be less gain for the workers.
97. The queen may be able to influence the ratio of investment in mass provisioning social bees because investment occurs at the time of egg laying.
98. M. V. Brian, *Colloq. Int. C.N.R.S.* **173**, 1 (1967).

[illegible] J. L. Pricer, *Biol. Bull. (Woods Hole)* **14**, 177 (1908). *Camponatus ferrugineus* specimens were captured in Delaware and killed and weighed by us (after drying) on 10 April 1975. *Camponotus pennsylvanicus* females were captured and killed in Stoughton, Mass., on 10 June 1974, dried, and weighed. (Males came from the Museum of Comparative Zoology collection.)

100. B. Hölldobler and U. Maschwitz, *Z. Vgl. Physiol.* **50**, 551 (1965).
101. M. Talbot, *Ecology* **29**, 316 (1948).

[illegible] ———, *ibid.* **24**, 31 (1943). *Prenolepis* reproductives overwinter as alates in the nest. Specimens were collected in mid-May while swarming in Lexington, Mass.

103. T. Lewis, *Trans. R. Entomol. Soc. London* **127**, 51 (1975).
104. M. Talbot, *Ann. Entomol. Soc. Am.* **44**, 302 (1951); A. E. Headley, *ibid.* **42**, 265 (1949). Specimens were collected from the nest 21 July 1974 at Blue Hills, Mass.
105. M. Talbot, *Contrib. Lab. Vertebr. Biol. Univ. Mich.* **69**, 1 (1954). Specimens collected 18 July 1974 at Wellfleet, Mass.
106. M. Autuori, *Arq. Inst. Biol. São Paulo* **19**, 325 (1950). No specimens were available for *A. bisphaerica*, so an approximate weight ratio of 8.0 was inferred from weights of the other two *Atta*.
107. M. Talbot, *Ann. Entomol. Soc. Am.* **38**, 365 (1945).
108. G. W. Elmes, *Oecologia (Berlin)* **15**, 337 (1974). At least 223 of the 596 males were apparently produced by laying workers, so that the ratio of investment is expected to lie near 1 : 2 (rather than 1 : 3).
109. M. V. Brian, personal communica[illegible]; ———, G. Elmes, A. F. Kelly, *J. Anim. Ecol.* **36**, 337 (1967). Weights (at swarming) are from Peakin (*35*).
110. B. Hocking, *Trans. R. Entomol. Soc. London* **122**, 211 (1970).
111. G. P. Markin, *Ann. Entomol. Soc. Am.* **63**, 1238 (1970). Each month of the year four nests were sampled at random and the contents were weighed.
112. G. W. Elmes, *J. Anim. Ecol.* **42**, 761 (1973).
113. Twenty-three nests, 1852 reproductives (*52*).
114. G. C. Eickwort and K. R. Eickwort, *J. Kans. Entomol. Soc.* **42**, 421 (1969).
115. T. H. Frison, *Trans. Am. Entomol. Soc. (Phila.)* **48**, 137 (1922).

1[illegible] R. W. Thorp, *Am. Midl. Nat.* **82**, 321 (1969).

117. P. F. Torchio and N. N. Youssef, *J. Kans. Entomol. Soc.* **41**, 289 (1968).
118. J. C. Porter, *Iowa State J. Sci.* **26**, 23 (1951).
119. P. F. Torchio, *Los Ang. Cty. Mus. Contrib. Sci.* **206**, 1 (1971).
120. G. C. Eickwort, *J. Kans. Entomol. Soc.* **40**, 42 (1967).
121. D. H. Janzen, personal communication.
122. G. C. Eickwort sexed pupae and prepupae in nests found prior to adult emergence in May 1972. He was unable to sex 27 prepupae. For additional data, see G. C. Eickwort, *Search* **3**, 1 (1973).
123. P. F. Torchio, personal communication.
124. Y. Hirashima, *Sci. Bull. Fac. Agric. Kyushu Univ.* **16**, 481 (1958).
125. C. D. Michener and R. B. Lange, *Ann. Entomol. Soc. Am.* **51**, 155 (1958).
126. S. D. Jayakar and H. Spurway, *Nature (London)* **212**, 306 (1966).
127. K. V. Krombein, *Proc. Biol. Soc. Wash.* **77**, 73 (1964).
128. O. Lomholdt, *Vidensk. Medd. Dan. Naturhist. Foren. Kbh.* **136**, 29 (1973).

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