Sex Ratio of Parental Investment in Colonies of the Social Wasp *Polistes fuscatus*

Abstract. *Field estimates of parental investment in the two sexes in the social paper wasp* Polistes fuscatus *indicate that the mother's interests, rather than those of her worker offspring, are realized. Local competition for mates seemed to be absent, and the population investment ratio was not significantly different from 1:1. Workers are not more closely related to the brood they tend than they would be to their own offspring. The 3/4 relationship between sisters in haplodiploid species cannot account for the maintenance of eusociality in this case.*

The sex ratio of parental investment in social wasp colonies bears on three current problems in social behavior: the importance of haplodiploidy in the evolution of hymenopteran eusociality (*1*), the resolution of queen-worker conflict in eusocial haplodiploid species (*2*), and the extent to which local mate competition favors female-biased sex ratios (*3, 4*). I now present data from field observations of colonies of the social paper wasp *Polistes fuscatus*, which suggest that when competition for mates is population-wide, the sex ratio of investment in reproductives is near 1:1.

Several features of *Polistes* social biology facilitate collecting data on behavior and sex ratios. Nests are founded annually by from one to several overwintered, inseminated females. The unenveloped nests allow direct observation of the behavior of individuals, including egg-laying, egg-eating, foraging, fighting, and mating. Workers emerge in midsummer, and reproductives in the late summer and fall. There are distinct behavioral (but no reliable morphological) differences between workers and reproductive females. The virtual lack of temporal overlap in their emergence, however, makes it possible to estimate sex ratios of reproductive individuals without extensive behavioral observations. The abundant nests are localized around houses and farm buildings, where mating and hibernation occur. It is possible, therefore, to gather sex ratio data for a sample of nests contributing to a local breeding population.

I collected sex ratio data for 17 of 20 nests known in a locality in southeastern Michigan. I determined the onset of emergence of reproductive females by observing daily the behavior of individuals on three of the nests. Foreign wasps were not permitted on the nest by workers. From the emergence of the first males and reproductive females to the end of the season, all new individuals on the nests were marked and recorded by sex every other day. While on the nests, wasps were marked with Testor's enamel, a procedure that did not seem to disrupt nest activities severely. The interval between markings was less than the average time spent by both males and females on the natal nest after eclosion, 4.7 days for males and 8.5 days for females (*5*). Any bias from individuals missed would probably underestimate investment in males.

To measure parental investment in each sex, one would need to know not only sex ratios but the time and energy spent plus risks taken by parents in behalf of male and female offspring, all of which would diminish their ability to invest in future offspring. I estimated the sex ratio of parental investment on nests by multiplying the sex ratio estimates by the relative wet weights (male divided by female) of 16 males and 23 females eclosing in the laboratory from a nest recently collected in the field. In addition to suffering from the general inadequacy of inferring parental investment from weights, this value probably underestimates investment in females, which stay longer on the parental nest and hence eat more after eclosion than do males. The females weighed 143 ± 3 mg, and the males weighed 135 ± 4 mg, yielding a wet weight ratio of 0.94 (*6*). Presumably, males were somewhat less than 94 percent as expensive as females to produce.

Table 1 gives the computed estimates of the sex ratio of parental investment for the 17 nests and for the population as a whole (*7*). Parental investment ratios were tested for deviation from 1:1 and 1:3 by comparing the observed sex ratios with sex ratios that would yield the theoretical investment ratios. The population investment ratio was not significantly different from 1:1 (χ^2 test, $P < .35$) but was significantly different from 1:3 ($P < .001$). Eight of the 17 nests produced investment ratios that deviated significantly from 1:1 ($P < .05$).

Fisher's theory of sex ratio selection (*8*) predicts that, when competition for mates is population-wide, parents will evolve to invest equally in the two sexes. Hamilton (*3*) showed that competition for mates within broods favors female-biased sex ratios of parental investment because the reproductive value of sons to their parents decreases when sons compete among themselves for females that one or a few of them could inseminate (*3, 4, 9*). I investigated the extent of mating among siblings by directly observing interactions on nests and by examining the spermathecae of females at various times after they eclosed. I observed one nest continuously during daylight hours when the wasps were active, from 10 August through 18 August 1976 (80 hours total). This was the time of peak abundance of males on nests. Males mounted females but rarely attached their genitalia. The evidence from dissections supported my impression that this behavior did not result in insemination: (i) Fourteen reproductive females captured as they left the nest for the first time were not inseminated. (ii) Two females collected 9 and 11 days after their eclosion were not inseminated. (iii) Only 2 of 29 reproductive females [distinguished from workers and foundresses by their thick fat deposits and lack of wing wear (*10*)] collected on nests in mid-September were inseminated. These data suggest that mating among siblings does not occur on the parental nest.

Mating aggregations, sometimes of more than 100 individuals, form near crevices and on tall sunlit structures such as buildings, telephone poles, and trees. Of 15 females collected from crevices in the fall, 11 were inseminated. Marked progeny of different nests appeared to mix freely (*11*), which suggests that Fisher's (*8*) assumption of population-wide competition for mates was met.

Fisher's theory (*8*) also assumes symmetry in the relatedness of parents to their male and female offspring. In the social Hymenoptera, queens are related to both sons and daughters by 1/2. Workers, which invest parentally in their mother's brood, are related to sisters by 3/4 (if the queen mated only once) and to brothers by only 1/4 because of the haplodiploid system of inheritance. Hamilton (*1*) argued that haplodiploidy predisposed the Hymenoptera to the evolution of sterile workers because females are potentially more closely related to their mother's brood than to their own offspring. Trivers and Hare (*2*) pointed out that this special relationship pertains only when colonial investment in reproductive members is female-biased. They suggested that opportunities for hymenopteran workers to capitalize on the asymmetry in their relatedness to brothers and sisters by investing preferentially in sisters may have increased the likelihood that eusociality would persist once it evolved. On this basis, they predicted

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that sex ratios of parental investment in eusocial hymenopteran colonies will be female-biased in a ratio of 1:3, unless laying workers contribute substantially to the male brood.

I observed the behavior of foundresses, workers, and reproductive offspring over the colony cycle on 20 nests from May through September 1974 through 1976 (approximately 400 hours). During 150 hours of observation in July, when workers and queens were on nests and reproductive broods were being produced, I did not see workers lay or eat eggs while the original queen was on the nest. Owen (*12*) and West Eberhard (*5*), in studies on the same population, also noted the absence of egg-laying and egg-eating by workers. Approximately half of 52 subordinate foundresses on multiple-foundress nests were also present while reproductive broods were being produced, but they contributed little to them. It appears that the reproductives reared on nests are chiefly offspring of the foundress queen.

Because queens are symmetrically related to male and female brood, and workers are not, their reproductive interests conflict in regard to the sex ratio of parental investment. This conflict has been linked to the broader issues of parent-offspring conflict and the origins of eusociality. Trivers and Hare (*2*) argued that workers should control the pattern of colony investment because they are the primary caretakers of the brood. They predicted that the way in which workers achieve their preferred ratio will depend on the cost to their inclusive fitnesses of confronting the queen aggressively. If a queen dies in such a fight, the workers lose a specialized egg-layer and source of closely related female eggs. They argued that this cost is less drastic in multiple-queen than in single-queen colonies because, there, workers can shift their investment to offspring of a closely related substitute queen. When workers can lay eggs nearly as well as the queen, as in *Polistes*, these arguments do not apply. The drop in worker relatedness to the brood after the queen's death is, in fact, greater in multiple- than single-queen colonies (*13*).

In contrast to Trivers and Hare (*2*), Alexander (*14*) and Trivers (*15*) have viewed the evolution of parent-offspring conflict in general as an uneven match favoring the parent. Alexander (*14*) has argued that parental care evolves so as to maximize the lifetime reproductive success of parents, not the inclusive fitnesses of particular offspring or sets of offspring. Thus, throughout the evolution of eusocial insect colonies, selection would have operated on queens to check tendencies in workers to maximize their inclusive fitnesses at the queen's expense. According to this argument, parents evolve to maximize their inclusive fitnesses, at the expense of offspring if necessary, and they will usually be able to achieve this end.

The almost exact coincidence of the population investment ratio with 1:1, and its significant departure from 1:3, in the absence of sibling mating competition on the nest, suggest that in *P. fuscatus* the queen's interests, rather than those of her worker daughters, are realized. Workers are not more closely related to the brood they tend than they would be to their own offspring. Haplodiploidy, therefore, cannot explain the maintenance of eusociality in this species (*2*). Kin selection (*16*), however (considering costs and benefits of altruistic behavior as well as the genetic relatedness of interactants), remains a possible explanation of worker altruism.

Although eight of the nests produced investment ratios significantly different from 1:1, they exactly canceled one another's effects on the investment ratio in the population as a whole. Therefore, their queens and workers should have suffered no counterselection on the basis of the devaluation of the more numerous sex (*8*).

Table 1. The sex ratio of parental investment in reproductives on single- and multiple-foundress nests in *P. fuscatus*. All sex ratio estimates were multiplied by a single estimate of the ratio of parental investment per individual of each sex [from wet weight at eclosion (*6*)]. Sex ratios are based on the number of male and female reproductives marked on each nest. It was usually not possible to mark every individual eclosing, as indicated by nest maps. The proportion of reproductives marked is estimated for each nest.

Reproductives marked (proportion)	Males : females (No.)	Investment ratio (male : female)
	Single-foundress nests	
0.8	40 : 80	1 : 2.12*
1.0	19 : 12	1 : 0.67
0.7	4 : 9	1 : 2.39
0.8	7 : 10	1 : 1.52
1.0	26 : 35	1 : 1.43
0.9	15 : 12	1 : 0.85
1.0	11 : 11	1 : 1.06
0.9	4 : 5	1 : 1.33
0.8	17 : 11	1 : 0.69
0.9	30 : 8	1 : 0.28*
0.8	7 : 15	1 : 2.27*
0.8	5 : 15	1 : 3.19*
	Multiple-foundress nests	
0.8	23 : 10	1 : 0.46*
0.9	123 : 32	1 : 0.71*
0.9	69 : 39	1 : 0.60*
0.5	4 : 5	1 : 1.33
0.9	20 : 36	1 : 1.91*
	Entire population	
	424 : 395	1 : 0.99

*Significantly different from an investment ratio of 1 : 1 (χ^2 test, $P < .05$).

A population-wide investment ratio of 1:1 might result from a balance between nests that are male- and female-biased in their investment patterns. For example, if certain proportions of nests are consistently orphaned before reproductive female eggs are produced, thus producing only males, queens might be selected to produce a female-biased investment ratio. They could thereby take advantage of the increase in reproductive value of females caused by the excess of males. This did not seem to be the case in the populations I studied. The queens of male-biased nests survived well beyond the time when the reproductive brood is usually complete. Nor was there any evidence of a worker's laying eggs in two of the male-biased nests that were observed regularly during July, the month of peak egg production (*5*). On one female-biased nest observed regularly, I saw no unusual strife between the queen and the workers nor any sign that the queen was dominated by the workers.

For several reasons, *P. fuscatus* colonies might be more likely to produce a 1:1 investment ratio than other species discussed by Trivers and Hare (*2*). The number of workers is small, usually less than 40. Workers are therefore less likely to realize their optimal sex ratio of parental investment by confronting the queen (*17*). Colonies are annual, and workers are reared almost entirely by foundresses. Queens are thus in a position to manipulate worker options by feeding them less as larvae than they might prefer. Queens probably mate multiply, so that the asymmetry in worker relatedness to brothers and sisters may be less than 1:3. The tendency for colonies to produce males earlier than reproductive females increases the expense to workers of modifying the colonial investment ratio in their own interests. When workers eclose, few female eggs and larvae are present. The males have usually completed part of their development and, therefore, have a higher reproductive value than contemporary eggs. This increases the costs to workers of discriminating against males or of replacing them with the workers' own male eggs (*18–20*).

Other characteristics of *Polistes* colonies make it more likely that workers will realize their optimal investment pattern. Because colonies are annual and there is only one reproductive brood, it may be easier for workers to assess the colony investment ratio and adjust their parental effort to optimize their inclusive fitnesses. Workers do not lay while the original queen is on the nest, so they should be strongly selected to bias their parental investment in favor of females.

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References and Notes

1. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964); *ibid.*, p. 17 (1964).
2. R. L. Trivers and H. Hare, *Science* **191**, 249 (1976).
3. W. D. Hamilton, *ibid.* **156**, 447 (1967).
4. R. D. Alexander and P. W. Sherman, *ibid.* **196**, 494 (1977).
5. M. J. West Eberhard, *Misc. Publ. Mus. Zool. Univ. Mich. 140* (1969).
6. Wide variation in the relative wet weight per individual of each sex produced on nests would undermine my estimates of the sex ratio of parental investment. Relative weights for a large sample of nests, needed to estimate the variance, were not obtained. Relative wing length data collected for 15 nests in 1974 suggest that inter-nest variation in this respect is not great. Wing length correlated significantly with body length in both sexes [males: $r^2 = .86$; females: $r^2 = .76$ (5)]. Wing length ratios ranged from 93 percent to 106 percent (males divided by females) averaging 98 ± 3 percent.
7. Estimating the population investment ratio by counting progeny of a random sample of nests departs from the χ^2 test's assumption of independent observations (here, individuals) when nests differ significantly from one another in their investment ratios. Sex differences in mortality and visibility, however, are likely to introduce errors in estimation after the termination of parental care. Thus, sex ratio data reported in the literature are often based on sampling by brood [for example (2); H. Howe, *Ecology* **57**, 1195 (1976); M. F. Willson, *Ecol. Monogr.* **36**, 51 (1966)]. The higher the proportion of all broods sampled, the smaller the effect of nonindependent sampling on the estimate. In view of the high proportion of known nests sampled in my study (0.85), the error introduced into the analysis by this departure from the assumptions is probably slight.

   Significant heterogeneity in investment patterns occurred in the pooled sample of nests (χ^2, $P < .001$). The proximate mechanisms by which differences in the sex ratio of parental investment are effected were not apparent in this study. I would expect them to be environmental cues at the time of egg-laying, which would influence queens to fertilize varying proportions of their eggs. It is possible, for example, that certain investment skews are associated with early or late production of reproductive offspring, the size of the worker force at a critical time, or the number of laying subordinate foundresses present. The precise control over the sex ratio afforded queens by haplodiploidy might allow them to track variations in the optimal sex ratio for their broods more closely than diplo-diploid parents. The long hazardous period of parental investment, with varying degrees of help from subordinate foundresses, and the production of sterile workers before any reproductive offspring undoubtedly increases the variety in circumstances to which egg-laying queens might respond.

   Whatever its proximal causes, heterogeneity in investment ratios among parents is predictable from sex-ratio theory. Fisher (8) argued that selection favors a particular ratio of investment in the population as a whole. Heterogeneity in the contributions of individual parents will not be selected against so long as the population investment ratio stays at its optimal value [(J. F. Crow and M. Kimura, *An Introduction to Population Genetics Theory* (Harper & Row, Evanston, 1970)].
8. R. A. Fisher, *The Genetical Theory of Natural Selection* (Dover, New York, 1958).
9. J. Maynard Smith, in preparation.
10. K. R. Eickwort, *Insectes Soc.* **16**, 67 (1969a).
11. On four occasions, males from two different parental nests were seen together in the vicinity of mating aggregations. On one occasion, progeny of at least four nests were seen together in a crevice where courtship and mating occurred.
12. J. Owen, thesis, University of Michigan (1962).
13. If the queen dies on a multiple-queen nest and is replaced by a sister, the workers must rear cousins instead of brothers and sisters. Their relatedness to the brood falls from 1/2 (assuming monogamy and a 1:1 sex ratio) to 3/16. If the queen dies on a single-queen nest and is replaced by a worker daughter, leaving the rest of the workers to rear nieces and nephews, the relatedness of the workers to the brood falls only half as much, from 1/2 to 3/8. Although such a nest would produce only males (because workers are uninseminated), it would have to flood the local breeding population with offspring to the point that male reproductive value was halved for the workers to suffer the same reproductive loss as the workers on the multiple-queen nest.
14. R. D. Alexander, *Am. Zool.* **12**, 648 (1972); *Annu. Rev. Ecol. Syst.* **5**, 325 (1974); in preparation.
15. R. L. Trivers, *Am. Zool.* **14**, 249 (1974).
16. G. C. Williams and D. C. Williams, *Evolution* **11**, 32 (1957); M. J. West Eberhard, *Q. Rev. Biol.* **50**, 1 (1975).
17. Mechanisms by which workers could forcibly affect the investment ratio are (i) by physically excluding the queen from cells after she has laid in them so she cannot eat or replace eggs or even assess the sex ratio of a brood and (ii) by keeping the queen from distributing food unequally to larvae, perhaps by preventing her from feeding them at all.
18. Colonies of *Polistes metricus* also produce males earlier than reproductive females [Metcalf and Whitt (19); Metcalf (20)]. Metcalf notes that this increases the expense to workers of discriminating against the queen's sons. Queens in *P. metricus* populations mate at least twice, using sperm from the two inseminations in a ratio of 9:1 (19). The sex ratio of investment in populations near Urbana, Ill., is approximately 1:1 (20).
19. R. A. Metcalf and G. S. Whitt, *Behav. Ecol. Sociobiol.* **2**, 339 (1977).
20. R. A. Metcalf, thesis, Harvard University (1975).

21. I thank J. Ehret, L. Frey, and C. Rosen for assistance in collecting data; R. D. Alexander, G. Borgia, D. P. Cowan, M. J. West Eberhard, T. E. Moore, D. Queller, D. Smith, and P. W. Sherman for comments on the manuscript; and the Theodore Roosevelt Memorial Fund and the University of Michigan for financial assistance.

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Frequency Discrimination Following the Selective Destruction of Cochlear Inner and Outer Hair Cells

Abstract. *Frequency discrimination was measured behaviorally before and after drug-induced lesions of cochlear hair cells in the cat. Discrimination was unaffected by complete loss of outer hair cells provided that at least 50 percent of inner hair cells were intact. Thus, inner hair cells are important for frequency discrimination, and they can function normally in this regard without the influence of outer hair cells.*

The role of the inner and outer hair cells of the cochlea in frequency discrimination is not clearly understood. There is evidence, however, for a difference in their roles in auditory behavioral threshold determination (1) and in cochlear frequency selectivity (2). As frequency discrimination or the detection of frequencies separated in time is a different task from frequency selectivity or the ability to separate the individual components of a complex signal, it is of interest to determine the relative roles of the inner and outer hair cells in frequency discrimination.

Our behavioral study was carried out on three monauralized cats trained to respond by a conditioned suppression technique (3), as this retains the advantages of classical reward-and-avoidance conditioning without the disadvantages. With this technique a steady baseline of responding (lick rate) was first established. A test stimulus, which termi-

Table 1. Behavioral thresholds, outer and inner hair-cell loss, and frequency discrimination after kanamycin administration.

Frequency (kHz)	Cat	Hair-cell loss (%)		Behavioral threshold changes (dB)	Frequency discrimination changes (F)
		Inner	Outer		
1	6	0	0	−8	4.04*
	8	0	0	−5	0.96
	10	0	0	7	0.80
4	6	0	0	0	0.79
	8	35	0	0	0.60
	10	25	0	−2	0.48
8	6	65	0	23	1.46
	8	100	0	22	0.65
	10	95	0	21	1.73
10	6	100	0	28	1.22
	8	100	5	26	0.86
	10	100	15	36	1.06
12	6	100	75	40	6.47*
	8	100	50	51	4.30*
	10	100	<100	49	2.57*

*For $F(9, 24) > 2.36$, $P < .05$.

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