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THE QUARTERLY REVIEW of BIOLOGY



ANT REPRODUCTIVE STRATEGIES AND SEX ALLOCATION THEORY

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ABSTRACT

Trivers and Hare (1976) predicted that the degree of genetic relatedness between hymenopteran workers and their brood is a fundamental factor in influencing the amount of resource allocated to the sexes. An analysis of a wide body of literature on ants (Family: Formicidae) strongly supports this genetic relatedness hypothesis (GRH). Their predictions on the differences in investment between monogynous, polygynous, slavemaking, and parasitic colonies are supported qualitatively and quantitatively both across and within species. Another explanation of female bias, local mate competition (LMC) (e.g., Alexander and Sherman, 1977), is found to be inconsistent with the data. The ratio of investment in species with non-conspecific brood care, most colonies producing either extremely male or female biased broods, as well as the suggestion that male ants may be highly limited in the number of females they can fertilize, are incompatible with LMC predictions. A limitation in the number of matings on the part of an individual male may mean that mating strategies in ant sexes could be quite different from those in most other species. The bimodal sexual investment pattern appears to be a mixed "evolutionary stable strategy and state" and seems proximately determined by the amount of food resources. Abundance favors females, scarcity favors males. Further utilization of game theory approaches may be quite useful in explaining both individual colony and population-level sexual investment values.

EDITORIAL NOTE

In this paper the following acronyms are used extensively:

GRH, the genetic relatedness hypothesis of the evolutionary mechanism that brings about shifts in the sex ratio in the groups under discussion;

LMC, local mate competition, both the phenomenon of competition among local males for mating with the queens and the hypothesis that this competition is responsible for the shifts in sex ratios observed.

The following phrases have a restricted meaning in the present context:

Male bias. Shifts of the sex ratio that result in more reproductive investment in male individuals.

Female bias. Shifts of the sex ratio that increase the proportion of female sexual individuals (discounting the neuter workers).

INTRODUCTION

A GENERAL question within biology concerns the relative amount of available resources animals should invest in the relative production of sons or daughters. Because a single male can potentially fertilize at least several females, a species would theoretically maximize its reproductive output by reducing its investment in males to a level where only enough males are produced to ensure that every female is mated. A seeming paradox exists: most species invest equally in producing males and females, and this sex ratio appears to result in an excess of males over what might be needed. Fisher (1930) explained this phenomenon as a consequence of parents being equally related to male and female offspring, so that the two sexes contribute equal numbers of genes to each generation. For if a population is female-biased, the average male will participate in producing more offspring than the average female. Consequently, parents that overproduce males will have more grandchildren than those that favor females. Genes for male production would then spread until both sexes were invested in equally. This elegant explanation was so powerful an argument that most species are now expected to invest equally, and those that do not merit special attention (Hamilton, 1967; Charnov, 1982).

One group in which female bias is often observed is the social Hymenoptera. An interesting facet of this group is that females are diploid and males are usually haploid (Crozier, 1977). With haplodiploidy, a female is equally related to sons or daughters, but is on the average three times more related to full sisters than to brothers (see Oster and Wilson, 1978, or Crozier, 1979, for a more complete description of hymenopteran genetics). Trivers and Hare (1976) proposed that this variation in genetic relatedness could be used for a simultaneous test of the Fisher theory of sex allocation and of the strength of kin selection. In species with a single queen (monogynous) per colony a possible conflict of interest exists. For the queens (the mothers) the population equilibrium is to invest equally in the two sexes, whereas the workers' (the sisters') equilibrium is a 3:1 female bias. Trivers and Hare (1976) predicted that because the work-

ers raise the brood, their equilibrium should actually prevail. They presented data which suggested that this was indeed the case. In polygynous species, investment ratios were closer to 1:1, as predicted by the reduction of the asymmetrical relatedness between the workers and their charges. In general, they concluded that the degree of genetic relatedness was a fundamental factor in generating the observed sex investment patterns, just as it is for non-haplodiploid species. These findings stimulated a number of theoretical papers on how hymenopteran societies may be structured, utilizing this genetic relatedness hypothesis (GRH) (for example, see Oster, Eshel, and Cohen, 1977; Oster and Wilson, 1978; Charnov, 1978; MacNair, 1978; Benford, 1978; Craig, 1980; Bulmer, 1981, 1983; Iwasa, 1981; Orlove, 1981; Pamilo, 1982a).

Nevertheless, the conclusions of Trivers and Hare have been far from unanimously accepted. Alexander and Sherman (1977) disputed whether the GRH was the basis for the sex ratio pattern. First, they objected to the methods used to analyze the data and to the assumptions about the ecology of several species. More importantly, they suggested that local mate competition (LMC) (Hamilton, 1967) was a more harmonious explanation. LMC describes a situation in which siblings compete among themselves for mates or breeding opportunities. For example, if a female's sons fertilize her daughters, she may maximize her fitness by producing only enough sons to ensure that all her daughters are fertilized. Under complete brother-sister mating, an equal numerical sex ratio is to be expected only if a male is capable of fertilizing only a single female. Alexander and Sherman also held that the extremely wide variance found in investment ratios among individual colonies within species was more indicative of a combination of LMC and local ecological factors than of genetic relatedness. Female-biased colonies were predicted as a result of LMC. Male-biased colonies were explained as a possible consequence of the queen's dying or running out of sperm. Darling (1978), after examining individual colony data, argued that GRH predictions were only sporadically supported. He correctly pointed out that because both processes pre-

dict a bias toward an excess of females, they could be acting simultaneously. Darling found the data on the whole to favor the hypothesis of local mate competition, mostly because the LMC hypothesis predicts only a general female bias and rarely a specific ratio of investment. In a later paper, Taylor and Bulmer (1980) derived an equation that did predict female bias quantitatively. This, however, was based on a knowledge of community structure, in terms of the number of other colonies with which sexuals from a given colony could be expected to interbreed. Such data have not been available and may be difficult to obtain.

In the time since the original papers by Trivers and Hare (1976) and Alexander and Sherman (1977), the controversy has not been adequately resolved. It may now be possible, however, to distinguish whether one, neither, or both hypotheses are consistent with observed fact. New data for a number of species have been collected. More important have been the advances in evolutionary theory. Game theory, with its resultant evolutionarily stable strategies and states (ESS's) has become a powerful incisive tool in explaining certain adaptations and behavioral strategies (Maynard Smith, 1982). Its use seems well suited to examining aspects of sex allocation theory (Charnov, 1982). This paper will attempt to explain sex ratios in ants by re-examining the data reviewed by Trivers and Hare as well as new data in a synthesis with the advances in evolutionary theory.

Because both hypotheses predict a bias favoring more females, the average investment in the sexes by a species cannot by itself accurately distinguish between the two hypotheses. They do, however, differ in predicting how the bias toward females is achieved within a species and the degree of such bias from species to species under various conditions (Table 1).

The genetic relatedness hypothesis (GRH) predicts that, under worker control, species with only one fertile queen per colony (monogynous) will show a 3:1 female investment bias, whereas polygynous species should show a significantly lessened bias. The local mate competition hypothesis (LMC) predicts a greater female bias in monogynous species, but the variance in the bias across species could be quite large, due to variance in severity of LMC. In essence, this hypothesis predicts only that investment be biased toward the female sex. If, however, the number of females that can be fertilized by a single male is known, then a numerical prediction may be possible. The GRH makes no numerical prediction except that the number of males should be such that, by investment (estimated as numbers $\times$ weight), the predicted female bias would be obtained. If males are very small in size relative to females, they should even outnumber females.

The LMC hypothesis predicts that non-conspecific brood care, such as slaves provide, should have no effect on the investment ratio, in and of itself. The phenomenon of

TABLE 1
Comparisons of predictions from hypotheses of genetic relatedness (GRH) and local mate competition (LMC)
 $\bar{R}$, proportion of resources invested in males, by weight; MPRE, numerical frequency of males.

Characteristic	GRH Prediction	LMC Prediction
Investment ratio (monogynous)	Female bias, 3:1 or $\bar{R} = 0.25$	Female bias ($0 < \bar{R} < 0.5$)
Investment ratio (polygynous)	Reduced or no bias $0.25 < \bar{R} \leq 0.5$	Reduced or no bias $0.25 < \bar{R} \leq 0.5$
Numerical sex ratio	No overall specific prediction	With singly mating males, MPRE = 0.5 in individual colonies
Variation in queen number within species	Polygynous colonies more male biased	Polygynous colonies more male biased
Non-conspecific brood care	No bias ($\bar{R} = 0.5$) irrespective of monogyny or polygyny	Degree of bias unchanged or greater female bias than shown by host species
Allowable range of investment ratios by individual monogynous colonies	$0 < \bar{R} < 1$ as long as the population average is at $\bar{R} = 0.25$	Narrower than GRH with $\bar{R} > 0.5$ rare in queenright colonies and MPRE = 0 rare because of male mating limitations

LMC does not directly depend on who tends the offspring. If conditions favorable for LMC are found in the slave species, then one should expect the same in the slavemakers. Slavemaking or parasitic species should not, as a group, show different investment patterns from those of species with similar gyny. The GRH predicts that equal investment in the sexes will occur in all species, for slaves raise the broods and because they are unrelated to the developing sexuals they have no preferred investment ratio. The observed investment ratio should therefore reflect the queens' equilibria of unity.

Finally, the LMC hypothesis is a phenomenon that must be expressed at the level of the individual colony. For LMC to affect investment ratios, breeding must occur within a restricted neighborhood, that is, a single colony, or only a few (Taylor and Bulmer, 1980). High variances in investment ratio are penalized because they would bias the neighborhood sex ratio away from the equilibrium (Verner, 1965; Taylor and Sauer, 1980). Producing too few males would mean that some females would not be mated, while producing too many would waste resources that could have been better invested in additional females. One therefore expects that most healthy colonies within a species or population should produce similar investment ratios and that the variance between these colonies would be low. GRH, an outbreeding phenomenon, can work at either the colony or population level, and the variance in investment ratios could be quite high.

Data from individual colonies have not been adequately examined to determine how the population average is attained. Darling (1978) examined individual-colony data for the prevalence of a predicted ratio, but did not consider the possibility of multiple strategies. Herbers (1979) did utilize a game-context approach, but her results were for only one population, and her assumptions may have been unnecessarily complex. This paper will analyze the data for evidence of a single or multiple investment strategies, and for the conditions under which those strategies are expressed.

SOCIAL SYSTEMS IN THE FORMICIDAE

This study is restricted to ants because all known species in the family Formicidae have

highly developed sociality, or in the case of parasitic species depend on the sociality of others (Wilson, 1971). This homogeneity reduces the problem of comparing factors involved in the evolution of the various stages of sociality and the selective pressures operating on a developed social system. Genetic relatedness and kin selection may have been involved in the origin of sociality, but other hypotheses such as mutualism or parental manipulation have been invoked in explaining primitively eusocial behavior (Lin and Michener, 1972; Starr, 1979). Therefore, it could be argued that in these species GRH effects may be obscured by other processes. Obligately, highly eusocial species, however, should provide a clear test of whether GRH can be expected to influence sex ratios in any Hymenoptera. Furthermore, LMC might also be apparent because the winged sexuals in ant species are poor fliers, a characteristic which may limit the distance they can travel and therefore the number of possible interbreeding colonies. Ant sexuals are also highly vulnerable outside the nest. Copulating within the nest would considerably reduce the amount of time females spend in searching for mates, and could greatly reduce the mortality risk associated with colony-founding.

Monogyny and polygyny are important distinctions for predicting relative investment in a sex. It is likely that most species, however, cannot be categorized as always being monogynous or polygynous, but instead fall into a continuum between the two extremes. For purposes of comparison, I shall nevertheless continue to place species exclusively in one category or the other, on the basis of either previous authors' descriptions or the predominant number of queens in the data sets used. This usage means that in any of the following analyses data from some polygynous colonies might be in the monogynous data set, and vice versa. In data sets where monogyny and polygyny are both common, comparisons within species will be examined.

Workers themselves laying viable male eggs may affect sex ratios (Oster, Eshel, and Cohen, 1977; Charnov, 1978; Benford, 1978). These authors have predicted that as the proportion of worker-produced males in monogynous species increases, the workers' equilibrium investment ratio will shift toward a more equal division between males and fe-

males. These papers also assumed that workers produce males in the presence of queens. Taylor (1981) assumed that workers produce males when the queen dies. He predicted that a process of compensation for colonies that could only produce males would result in a reduction of female bias on the level of the population. The extent to which workers do lay eggs is not known, but it certainly appears to be more common than was assumed by Trivers and Hare (for evidence in just the genus *Myrmica* see Brian, 1953, 1969; Weir, 1959; Elmes and Wardlaw, 1981). The origin of the males unfortunately cannot be conclusively determined in the data set reviewed, and hence I must assume that all males are the sons of the queens. The effects of the prior two assumptions on the predicted results will be discussed later.

For their predictions about monogynous species, Trivers and Hare (1976) assumed that females either mate with only one male or that sperm from multiple matings would clump, so that at any time most worker cohorts would derive from the same father. If sperm were to mix and be used randomly, the average relatedness between sisters would decrease. Sister-brother relatedness, however, is unaffected by multiple mating. Simultaneous use of more than one male's sperm should therefore result in lessened female investment bias by the workers. The degree to which sperm do clump in ants is poorly known. In other Hymenoptera, however, there is evidence that sperm come predominantly (but not exclusively) from only one male at a time (see review by Crozier and Brückner, 1981). In order to adjust GRH predictions accurately, one would need to know both the probability of a female mating multiply and, if multiply-mated, the degree of sperm-mixing. Unfortunately, the data are too poor to make any reasonable estimates. I will therefore assume that conditions in monogynous colonies approximate the predictions based on the use of only one male's sperm. The error in doing so may be small. Monoandry (a single father per colony) has been suggested as occurring in several ant species (Crozier, 1973; Hung and Vinson, 1976; Pamilo, 1982b) and, in any case, polyandry may have little effect relative to that of other factors such as polygyny (Pamilo, 1982b).

Males of most animal species seem to be

capable of fertilizing more than one female. Under conditions of LMC and with both sexes of roughly equal size, this hypothesis predicts a numerical excess of females (e.g., one brother can fertilize many sisters). But for this situation to be true in ants, males ought to be able to mate multiply. Most investigators who have studied post-copulatory behavior in ants have concentrated almost exclusively on the actions of the female. There is, however, considerable evidence that in a wide variety of species the males may have only a limited number of matings. *Pheidole pallidula* males die immediately after mating (Goetsch, 1957), and *P. sitarches* males make no effort for second copulations and rapidly fall prey to predators (Wilson, 1957). *Solenopsis invicta* males probably copulate only once during their mating flights (Ball and Vinson, 1983). Males of attine species die on the day of their natal flight (Weber, 1972). *Pogonomyrmex occidentalis* males are often found with severe wounds on the gaster attributable to females gnawing at them to terminate copulations (Nagel and Rettenmeyer, 1973). In *P. barbatus*, *P. desertorum*, *P. maricopa*, and *P. rugosus*, males compete intensely between themselves for access to females and remain in copulation until the females bite their gasters. Females are frequently found with male copulatory organs attached (Hölldobler, 1976; Markl, Hölldobler, and Hölldobler, 1977). Marikovsky (1961) found similar behavior in *Formica rufa*, where females regularly bit off the abdomen of mating males. *F. subintegra* males have been observed to mate several times, although females terminate copulation by biting behavior (Kannowski, 1963). *F. pergandei* females chew the abdomens and sometimes the heads off of males after copulating (M. R. Gross, pers. commun.). In *F. polycytena* many males are required to fertilize just a few females and the males die soon after mating (Goesswald, 1978). In *Harpagoxenus sublaevis*, individuals have been shown to be capable of multiple mating. In a laboratory situation, these males can mate ten times in an hour, but in the closely related species *H. canadensis*, few males can participate in two copulations and none in more than two (Buschinger and Alloway, 1979).

There may be several reasons why males have evolved to mate only once. Females store

sperm, and a male's contribution can possibly produce offspring for an extended period of time. The transfer of sperm is not limited by the female's storage capacity, which seems to exceed the maximum amount of sperm a single male can transfer at a given time. Kerr (1961) and Wilson (1971) have documented how many times females have mated by the amount of sperm they contain and Pamilo (1982b) through genetic analysis of colony members found evidence that more than one male's sperm was being used. Males may have very little reason to "hold back" sperm for any future copulations, for the use of stored sperm means that, on average, males that give all their sperm to a single female will leave no fewer offspring than those that divide their sperm between more than one female. In fact, the latter practice may be less successful, since there is always a finite probability that a male might die between his first and any subsequent copulations. This is especially true if the mating occurs outside of the nest. Males might be able to produce more sperm between matings, but to my knowledge no study has looked at the rate of sperm replenishment in ants. It seems unlikely to me that it could offset the mortality of the males. Therefore, on average, a multiple-mating strategy may pass less sperm to females.

Furthermore, if the female is successful in founding a colony, the initial broods will tend to be exclusively workers (and therefore non-sexual) because the colony must first pass through a growth phase (Oster and Wilson, 1978; Brian, Clarke, and Jones, 1981). If sperm clump, the fewer with which a male inseminates a female, the higher the likelihood that they may be used in worker production (a genetic dead-end), and fail to contribute to any sexual offspring. Thus the optimal male strategy may be to maximize the number of spermatozoa passed in the first copulation. Males may attempt to gain further copulations, possibly, only if such do not reduce the success of the first one. It is predicted, therefore, that due to selection pressures favoring single mating, males of most species are incapable of mating more than once or twice even under ideal (i.e., laboratory) conditions.

The evidence supporting the single-mating pattern suggests that LMC theory will

not predict a numerical superiority of female progeny in ants, as it might with other systems. If males do mate singly, then one must expect roughly 50 per cent or more of a colony's sexuals to be male. If LMC is important, numerical sex ratios biased toward females would mean that a number of females will remain unmated. The effects of LMC, therefore, may be expressed in biomass akin to the predictions on the basis of GRH (i.e., make large females, not many).

COMPARISON OF GRH AND LMC

The predictions of the GRH and LMC hypotheses (Table 1) and the observed data (Table 2) can be examined in detail point by point.

A. Investment Ratios

The investment of a species in males ($\bar{R}$) was calculated for both monogynous and polygynous species as the biomass of males produced divided by the total biomass of sexual offspring. Therefore, if $\bar{R} = 0.5$, a species invests equally, by weight, in both sexes, while $\bar{R} = 0.25$ means a female bias of 3:1 in terms of resources allocated to sexual individuals. Investment data were obtained from the literature for 33 monogynous and 12 polygynous species (Table 3, and Fig. 1). The average investment in males for monogynous species is 0.282 and for polygynous species 0.522 (values significantly different by the Mann-Whitney U test, $t = 3.953$, $p < 0.001$). Little overlap exists between the two groups, as 21 of 33 (64%) of the monogynous species have more female-biased investment ratios than the most biased polygynous species (see Fig. 1).

Ward (1983) examined investment ratios in three species of ponerine ants: *Rhytidoponera confusa*, *R. chalybaea*, and *R. purpurea*. I included only the last-named species in the statistical analysis because the first two reproduce both by colony fission and by release of individual sexuals. In the first two of these species it was difficult to determine a population investment ratio because of the difficulty in quantifying the investment in the female function by colonies that reproduced by budding (Ward, 1983). Ward estimated an overall investment ratio for all three species as falling between $0.224 \leq \bar{R} \leq 0.335$.

TABLE 2

Observed data and conclusions about accuracy of predictions by genetic relatedness (GRH) and local mate competition (LMC) hypotheses

Characteristic	Observed	Conclusion
Investment ratio (monogynous)	$\bar{R} = 0.282$	GRH strongly supported but LMC cannot be rejected
Investment ratio (polygynous)	$\bar{R} = 0.522$	Both supported
Numerical sex ratios	MFRE = 0.579 (monogynous) MFRE = 0.687 (polygynous)	Inconsistent with LMC, MFRE variance in individual colonies is too large
Variation in queen number within species	Polygynous colonies show reduced female bias	Consistent with both although biology of species examined does not suggest LMC
Non-conspecific brood care	$\bar{R} = 0.545$; female bias always less than in hosts	Consistent with GRH and inconsistent with LMC
Allowable range of investment ratios by individual monogynous colonies	Sexual specialist colonies predominate; investment pattern clearly bimodal	Male specialists inconsistent with LMC as might be female specialists as well but pattern easily reconciled with GRH

Investment ratios in monogynous and polygynous species are very close to the values predicted by Trivers and Hare. The data are particularly impressive in the light of so wide a range of numerical sex ratios, expressed as the mean frequency of males (MFRE), producing the expected investment ratios. For example, in *Prenolepis imparis*, MFRE = 0.886, but the reproductive investment in males is $\bar{R} = 0.234$. As Alexander and Sherman (1977) and Darling (1978) have cogently argued, the LMC hypothesis may also produce this ratio. Taylor and Bulmer's (1980) model of sexual investment as affected by LMC does provide a quantitative prediction. To produce that observed investment average of $\bar{R} = 0.282$, however, in the monogynous species one would have to assume that the average size of a breeding group would be 2.69 colonies. For most of the species examined this assumption may be unreasonably low unless extensive mating occurs within the nest. This possibility will be considered further in discussing the individual colony data. Nevertheless, while the genetic relatedness hypothesis is strongly supported by these data, the LMC hypothesis cannot be rejected.

B. Numerical Sex Ratios

Male frequency is expressed as the number of males divided by the total number of sex-

uals in each species. The mean frequency of males (MFRE) was 0.579 and 0.687 for 34 monogynous and 15 polygynous species, respectively (see Table 3 and Fig. 2). The distribution of means differs at a marginally significant level (Mann-Whitney U test, $t = 1.779$, $0.05 < p < 0.1$), but they are not as cleanly separated as the investment distributions. Both groups had a large percentage of species exhibiting an MFRE near 0.5 (i.e., a 1:1 sex ratio). Although polygynous species as a group are male-biased, they show a large spike in the number of species found at a 1:1 sex ratio, for 7 of the 15 species have between 40 per cent and 60 per cent male populations. The frequency of males supports the earlier hypothesis, as well as the observations, that males are limited in the number of females they can fertilize.

If the single-mating hypothesis is true, it is then apparent that the LMC hypothesis cannot operate according to the conventional assumption that one male is capable of fertilizing many females. As already pointed out, single mating implies that numerical sex ratios must be close to equality. On a population or species level, sex ratios appear to support this prediction. The LMC hypothesis, however, further predicts that 1:1 sex ratios must be found within individual colonies, as well as species-wide. This prediction will therefore be tested within the data for individual colonies.

TABLE 3

Summary of sexual production in individual species

F/M, weight of the average female divided by weight of the average male. $\bar{R}$, the proportion of sexual resources invested in males (measured as their total biomass divided by total sexual biomass). MPRE, the numerical frequency of males in the total population.

Monogynous Species [Source(s)]	Males	Females	F/M	$\bar{R}$	MPRE
<i>Acromyrmex octospinosus</i> [Lewis (1975); T/Ha]	2127	2363	2.50	.265	.474
<i>Aphaenogaster rudis</i> [Headley (1949); Talbot (1954); T/H]	305	56	12.71	.300	.845
<i>A. treatae</i> [Talbot (1951); T/H]	1180	694	10.11	.144	.630
<i>Apterostigma dentigerum</i> [Forsyth (1981)]	285	269	1.02	.509	.514
<i>Atta bisphaerica</i> [Autuori (1950); T/H]	26610	8439	8.00 ^b	.283	.759
<i>A. laevigata</i> [Autuori (1950); T/H]	16852	5871	8.37	.255	.742
<i>A. sexdens</i> [Autuori (1950); T/H]	99632	20513	7.67	.388	.829
<i>Camponotus ferrugineus</i> [Pricer (1908); T/H]	1043	811	6.52	.165	.563
<i>C. herculeanus</i> [Hölldobler & Maschwitz (1965); T/H]	4500	1800	5.33	.319	.714
<i>C. pennsylvanicus</i> [Pricer (1908); T/H]	542	707	6.84	.101	.434
<i>Formica fusca</i> [Darling (1978)]	283	112	2.78	.476	.716
<i>F. pallidefulva nitidiventris</i> [Talbot (1948); T/H]	348	1153	1.82	.142	.232
<i>Lasius alienus</i> [Brian (1979)]	91540	17200	17.12	.237	.842
<i>L. flavus</i> [Pickles (1940)]	1232	486	18.90	.118	.717
<i>L. niger</i> [Boomsma, Van der Lee & Van der Have (1982)]	89618	23953	11.83	.240	.789
<i>Leptothorax ambiguus</i> [Talbot pers. commun. to T/H]	76	93	6.30	.115	.450
<i>L. curvispinosus</i> [Headley (1943); T/H]	221	138	4.53	.261	.616
<i>L. longispinosus</i> [Headley (1943); Herbers (1984); T/H]	924	520	2.63	.403	.640
<i>Myrmecina americana</i> [Talbot pers. commun. to T/H]	123	103	2.62	.313	.544
<i>Myrmica ruginodis</i> (macrogyne) [Brian & Brian (1951); Mizutani (1981); Elmes, pers. commun.]	3877	4568	1.54 ^c	.355	.459
<i>M. schencki</i> [Talbot (1945a); T/H]	187	608	2.00	.133	.235
<i>M. sulcinodis</i> [Elmes (1974) & pers. commun.]	2386	1325	1.52	.542	.643
<i>Pogonomyrmex montanus</i> [MacKay (1981)]	5996	5731	2.49 ^d	.296	.511
<i>P. rugosus</i> [MacKay (1981)]	1247	470	3.73 ^d	.416	.726
<i>P. subnitidus</i> [MacKay (1981)]	1312	556	4.53 ^d	.342	.702
<i>Prenolepis imparis</i> [Talbot (1943); T/H]	1780	229	25.40	.234	.886
<i>Pseudomyrmex belti</i> [Janzen (1975)]	399	323	1.88	.397	.553
<i>P. ferruginea</i> [Janzen (1975)]	144	320	1.70	.209	.310
<i>Rhytidoponera purpurea</i> [Ward (1983)]	1425	1632	2.44	.264	.466
<i>Sericomyrmex urichi</i> [Weber (1969, 1972)]	201	343	2.91	.168	.369
<i>Stenamma brevicorne</i> [Talbot (1975); T/H]	88	121	2.44	.229	.421
<i>S. diecki</i> [Talbot (1975); T/H]	267	212	3.47	.266	.557
<i>Tetramorium caespitum</i> [Brian, Elmes & Kelly (1967); Brian (1979)]	22643	19668	1.57	.423	.535
<i>Trachymyrmex septentrionalis</i> [Cole (1939); Weber (1972)]	395	895	--	--	.306
AVERAGE				.282	.579
S. D.				±.12	±.18
Polygynous Species [Source(s)]	Males	Females	F/M	$\bar{R}$	MPRE
<i>Atta texana</i> [Moser (1963, 1967)]	1080	875	--	--	.552
<i>A. vollenweideri</i> [Jonkman (1980)]	7014	657	--	--	.914
<i>Crematogaster mimosae</i> [Hocking (1970); T/H]	7223	638	10.41	.524	.920
<i>C. nigriceps</i> [Hocking (1970); T/H]	2089	829	4.21	.374	.716
<i>Formica obscuripes</i> [Clark & Comanor (1972); Herbers (1979)]	6060	5703	1.44	.425	.515
<i>F. pallidefulva incerta</i> [Talbot (1948); T/H]	346	427	1.82	.308	.448
<i>Myrmica rubra</i> [Brian (1972); Elmes (1976)]	3490	417	1.51	.847	.893
<i>M. ruginodis</i> (microgyne) [Mizutani (1981); Elmes pers. commun.]	859	122	1.54	.821	.876
<i>M. sabuleti</i> [Brian (1972); Elmes pers. commun.]	10274	2366	1.58	.733	.813
<i>M. scabrinodis</i> [Elmes pers. commun.]	147	145	1.53	.391	.503
<i>Pheidole pallidula</i> [Passera pers. commun. to T/H]	1595	257	5.58	.527	.861
<i>Pseudomyrmex nigrocincta</i> [Janzen (1975)]	1173	860	1.93	.415	.577
<i>P. nigropilosa</i> [Janzen (1975)]	200	113	1.86	.486	.639
<i>P. venefica</i> [Janzen (1973)]	2962	2808	--	--	.513
<i>Tetraponera penzancei</i> [Hocking (1970); T/H]	268	201	1.94	.408	.571
AVERAGE				.522	.687
S. D.				±.18	±.18
Slavemakers or Parasites [Source(s)]	Males	Females	F/M	$\bar{R}$	MPRE
<i>Formica talbotae</i> [Talbot (1976)]	330	263	1.11 ^e	.532	.556
<i>Harpagoxenus americanus</i> [Wesson (1939)]	346	165	1.75 ^f	.545	.677
<i>H. sublaevis</i> [Buschinger pers. commun. to T/H]	1426	1033	1.73	.446	.583
<i>Leptothorax duloticus</i> [Wesson (1940); Talbot (1957); T/H]	1131	489	2.00	.536	.698
AVERAGE				.515	.628
S. D.				±.05	±.07

TABLE 3 (continued)

- (a) T/H = Trivers and Hare (1976), means that their male and female weights were used. They often used dry weights of museum specimens. The other weights are fresh weights from the literature, if possible, associated with the data sets used. Trivers and Hare found that males lost more weight proportionally than females when dried. Therefore, if only dry weights could have been used, slightly more female biased R's would have been expected.
- (b) Ratio estimated by Trivers and Hare (1976) from other *Atta* species.
- (c) Ratio estimated by present author from other *Myrmica* species worked on by G. W. Elmes.
- (d) Ratio of caloric value content of females to males.
- (e) Dry weight average of 2 females and 2 males (kindly provided by E. O. Wilson).
- (f) Weight ratio estimated as approximating *Harpagoxenus sublaevis*, from which it is not grossly different. However, the morphometry of this species may be more like *Leptothorax duloticus* and the species may be soon reclassified (Buschinger and Alloway, 1978). In that case, the estimate ought perhaps to be closer to 2.00 and would result in $R = 0.512$.

C. Intraspecific Monogyny and Polygyny

A number of species have both monogynous and polygynous colonies. In fact, as more species are closely examined it may turn out that very few of them are always strictly monogynous or polygynous. The genus *Myrmica* seems to have a number of species in evolutionary transit between polygyny and monogyny (Elmes, 1980). *Myrmica ruginodis* has both monogynous macrogyne and polygynous microgyne varieties (Brian and Brian, 1955). *M. sabuleti* has been classified as a polygynous species (Brian, 1972), but in the data sets examined in this paper, 55 out of 126 colonies had only a single queen. Conversely, *M. sulcinodis* has been considered monogynous (Elmes, 1974), but 37 of its 104 colonies examined were polygynous. *Formica pallidefulva* has two varieties, *nitidiventris* which is

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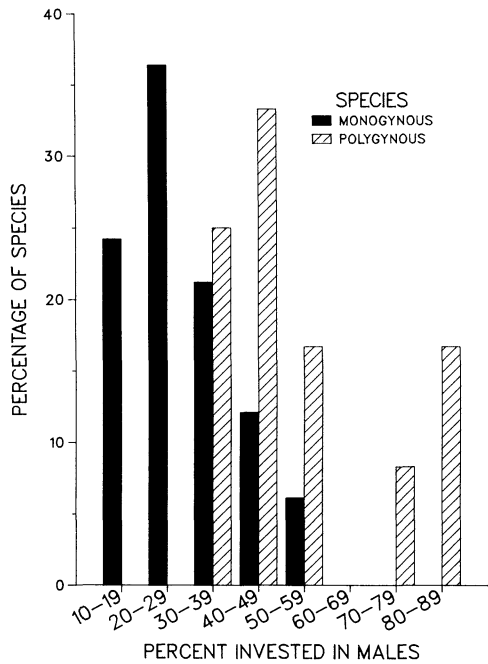


FIG. 1. PERCENTAGE OF INVESTMENT IN MALES ($\bar{R} \cdot 100$) BY MONOGYNOUS AND POLYGYNOUS SPECIES

The mean for monogynous species is 28.2 ± 4.1 (2 S.E.); for polygynous species, 52.2 ± 10.5 .

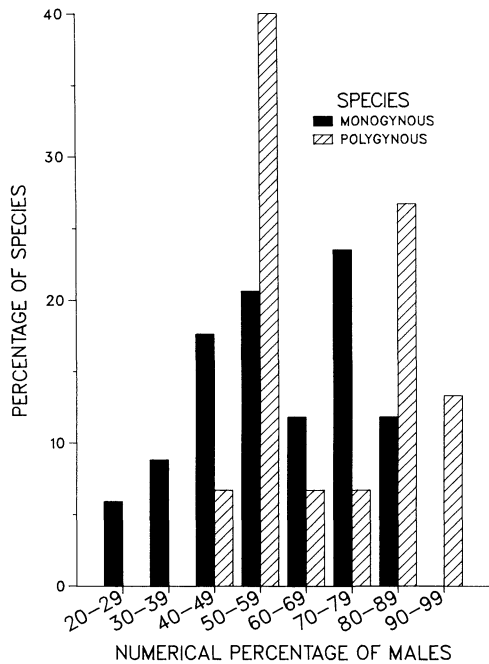


FIG. 2. THE AVERAGE PERCENTAGE OF MALES (MFRE $\cdot 100$) IN MONOGYNOUS AND POLYGYNOUS SPECIES

In monogynous species the mean = 57.9 ± 6.1 ; in polygynous species, 68.7 ± 9.0 .

monogynous, and *incerta* which is polygynous (Talbot, 1948). These four species can be examined to see whether there is a difference in the amount invested in males across colony type but within species.

In all four species the polygynous colonies invested more greatly in male offspring (larger $\bar{R}$'s) than did monogynous ones (see Fig. 3). Although both hypotheses predict an increased bias toward more males, the biology of the *Myrmica* species suggests that LMC is not very important here. These species tend to be common, and have numerous opportunities for an interaction and exchange of sexuals between colonies (Brian, 1956; Elmes, 1978, 1982; Elmes and Wardlaw, 1982a). Queens can be caught outside of the colony at any time during the active season (Elmes, 1982). Queens also seem to be short-lived, and colonies without queens probably recruit new ones (Elmes, 1980). The apparent high degree of outcrossing and movement of sexuals between colonies suggest rather little local mate competition, but the genetic relatedness hypothesis still predicts a reduced bias toward more males under monogyny. Furthermore, the high number of colonies with apparently fertilized queens producing extreme bias toward more males is inconsistent with an LMC effect although not with GRH, as will be shown later.

Herbers (1984) studied a population of *Leptothorax longispinosus* in which 32 per cent of the colonies were polygynous. She found an increasing bias toward excess of female in individual colonies in the following order: queenless > monogynous > oligogynous (2-4 queens) > polygynous (5 or more queens). This order was considered to support the genetic relatedness hypothesis. Queenless colonies were probably polydomous (that is, adjacent nests cooperate to some extent and are likely the result of fission within a single colony) and are autonomously functioning extensions of monogynous colonies. Most or all of the eggs seemed to be queen-laid. In these colonies there was assumed to be no worker-queen conflict, and the monogynous worker equilibrium appeared to be reflected ($\bar{R} = 0.250$). As functional queen number increases, the queen and worker equilibria converged. In accordance with this predic-

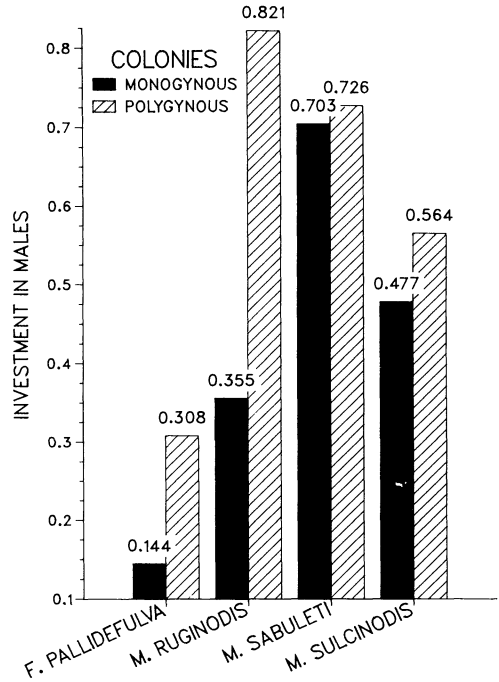


FIG. 3. THE AVERAGE INVESTMENT IN MALES ($\bar{R}$) BY MONOGYNOUS AND POLYGYNUS COLONIES WITHIN A SINGLE SPECIES

On the average, male bias is seen to be greater in the polygynous colonies.

tion, Herbers found that $\bar{R} = 0.564$ in polygynous colonies.

Another species that has both monogynous and polygynous social organization is *Solenopsis invicta*. Trivers and Hare (1976) listed it as monogynous, but the queen number actually varies geographically (see Fletcher, 1983, for review). In Mississippi, about 50 per cent of the colonies are polygynous (Glancey, Craig, Stringer, and Bishop, 1973; Fletcher, Blum Whitt, and Temple, 1980); and Morrill (1974) found that 52 per cent of the alates in flights were female. This ratio translates to an $\bar{R}$ of 0.353 (weights from Markin and Dillier, 1971). Markin and Dillier estimated $\bar{R}$ as 0.352 and a sex ratio close to 1:1 in northern Florida. Although no polygynous colonies have yet been found in that area, the workers do care for newly mated queens (Adams, Banks, and Plumley, 1976), and queenless colonies readily accept new queens (Tschin-

kel and Howard, 1978). Bass and Hays (1979) found in Bowman, South Carolina, 2.6 males per female alate, a ratio that translates to $\bar{R} = 0.606$. It would be an interesting test of predictions from the genetic relatedness hypotheses to see whether investment in males increases as the asymmetry in relatedness between workers and their sisters and brothers decreases owing to different social structures. *S. invicta* is a poor candidate for local male competition because mating occurs in simultaneous large flights from numerous colonies (Markin and Dillier, 1971; Morrill, 1974; Bass and Hayes, 1979).

D. Non-Conspecific Brood Care

The two hypotheses lead to quite different predictions for the investment ratios in situations where no conspecific workers are involved in brood care. GRH predicts that the usurping queen's desired equal investment in both sexes will be expressed. In these species, inasmuch as the workers are unrelated to their sexual brood, any manipulation by them of the sex ratio would have no effect on their own fitness. The slavemaker or parasitic queen, however, can increase her fitness by producing an investment ratio of unity. In this asymmetrical situation, the queen can be selected to manipulate the workers, but they cannot be selected to resist manipulation.

The LMC hypothesis predicts that the observed investment ratio should be independent of who raises the brood. Under local male competition, a female-biased sex ratio equally benefits both the queen and the workers, and the investment equilibrium should be unaffected by non-conspecific brood care. Furthermore, slavemakers and parasites, by their very nature, may in general be rarer than their hosts. With rarity it might take longer and be more difficult to encounter mates from unrelated colonies, a situation that could favor close-kin mating. If so, LMC might be greater in these slave or parasite species than in their hosts. It would be predicted that any changes in the investment ratio are then more likely to produce a bias toward females in excess of that manifested in the hosts.

There are data for three slavemakers: *Harpagoxenus americanus* (Wesson, 1939), *H. sub-*

laevis, and *Leptothorax duloticus* (Trivers and Hare, 1976), and for one worker-less parasitic species, *Formica talbotae* (Talbot, 1976). The average $\bar{R}$ for the four species is 0.515, and no species is less biased against production of males than $\bar{R} = 0.446$ (see Table 3). Their distribution of mean $\bar{R}$'s is significantly different from that of monogynous species (Mann-Whitney U test, $t = 2.984$, $p < 0.01$), but not from that of polygynous species ($U = 33$, $p > 0.1$). The slavemakers attack both *Leptothorax curvispinosus* and *L. longispinosus*. These two species have $\bar{R}$'s of 0.261 and 0.403, respectively, which are below the investment in males exhibited by any of the three slavemakers. In all five species, most colonies are monogynous. *F. talbotae* is a parasite of *F. obscuripes* and both species are polygynous. *F. talbotae* has an $\bar{R}$ of 0.532, while in *F. obscuripes* $\bar{R} = 0.425$. In all, the data clearly are in agreement with the genetic relatedness hypothesis and local male competition seems a very poor explanation of investment ratios.

E. Analysis of Individual Colonies

For 22 monogynous, 6 polygynous, and 1 slavemaking species the investment in males could be examined colony by colony. Immediately obvious was the bimodality evident in the investment. Although the average investment in males is 0.279 and 0.588 for the monogynous and polygynous species, respectively, in both groups most colonies were either male or female specialists (Table 4; Fig. 4). This trend is almost ubiquitous (*Tetramorium caespitum* is the only obvious exception). The polygynous species are distinguished from monogynous ones by having relatively more male and fewer female specialist colonies.

This tendency for specialization has been noted by several authors in studies where precise numbers of sexuals were not published. In *Solenopsis invicta*, 78 out of 150 mounds had one sex predominating by a ratio of 10:1 or greater (Markin and Dillier, 1971). Bass and Hays (1979) found similar results with this species. Talbot (1945b) found that 10 of 15 *Lasius neoniger* colonies she examined were extremely biased toward one sex. In *Formica obscuripes*, 11 of 15 colonies produced flights of alate sexuals in which almost all were of one

TABLE 4

Data from species for which colonies were individually reported

The total ranges (0.0 - 1.0) of investment in males (R) and frequency of males (MPRE) are divided into six equal-sized categories. The first number in each column refers to the number of colonies which fall into the range of investment values specified by that category. The second number is the number of colonies that show MPRE values within the same category. This means, as an example, that for *Aphaenogaster rudis* seven colonies had extremely male-biased investment ratios ($.834 \leq R \leq 1.0$) and eleven colonies produced males within the same frequency range ($.834 \leq \text{MPRE} \leq 1.0$).

	RANGES OF R/MPRE					
	Extreme Female Bias	3:1 Female Bias	No Bias	No Bias	3:1 Male Bias	Extreme Male Bias
MONOGYNOUS SPECIES	0.0-.166	.167-.333	.334-.500	.501-.666	.667-.833	.834-1.0
<i>Aphaenogaster rudis</i>	1/0	4/0	0/1	1/0	1/2	7/11
<i>A. treatea</i>	6/0	2/2	1/1	0/3	0/2	3/4
<i>Atta bisphaerica</i>	1/0	2/0	2/2	0/1	0/1	0/2
<i>A. laevigata</i>	1/0	3/0	0/0	2/3	0/1	0/2
<i>A. sexdens</i>	4/0	1/0	2/0	0/3	0/1	0/3
<i>Camponotus ferrugineus</i>	5/1	0/1	0/1	0/2	0/0	1/1
<i>C. pennsylvanicus</i>	4/0	0/0	0/4	0/0	0/0	0/0
<i>Formica fusca</i>	6/5	1/1	1/0	1/1	0/1	9/10
<i>F. pallidefulva nitidiventris</i>	14/14	0/0	0/0	0/0	1/1	4/4
<i>Lasius flavus</i>	2/1	0/1	2/0	2/0	0/0	4/8
<i>Leptothorax curvispinosus</i>	5/5	0/0	1/0	0/0	1/1	3/4
<i>L. longispinosus</i>	6/4	2/1	1/2	0/1	1/1	3/4
<i>Myrmica ruginodis</i>	7/5	6/3	2/6	1/2	1/0	15/16
<i>M. schencki</i>	7/6	1/1	0/1	1/1	0/0	1/1
<i>M. sulcinodis</i>	21/19	8/6	6/5	4/7	1/3	64/64
<i>Pogonomyrmex montanus</i>	16/10	3/8	6/0	5/7	4/5	1/5
<i>P. rugosus</i>	1/0	0/0	0/1	1/0	0/1	2/2
<i>P. subnitidus</i>	1/0	1/0	1/1	1/0	2/2	1/4
<i>Prenolepis imparis</i>	3/1	5/1	1/0	0/2	0/1	3/7
<i>Stenamma brevicorne</i>	4/3	1/1	0/0	1/1	0/1	2/2
<i>S. diecki</i>	2/2	6/0	0/1	0/5	0/0	2/2
<i>Tetramorium caespitum</i>	12/9	22/11	15/23	17/12	10/18	4/7
TOTAL	129/85	68/37	39/47	39/52	22/42	129/163
POLYGYNOUS SPECIES	0.0-.166	.167-.333	.334-.500	.501-.666	.667-.833	.834-1.0
<i>Formica obscuripes</i>	10/9	9/9	3/2	3/3	4/5	15/16
<i>F. pallidefulva incerta</i>	8/8	1/0	0/1	0/0	1/1	2/2
<i>Myrmica rubra</i>	0/0	1/0	0/1	1/0	0/1	9/9
<i>M. ruginodis</i>	0/0	1/1	0/0	1/1	1/0	5/6
<i>M. sabuleti</i>	10/9	7/2	6/9	4/7	7/6	92/93
<i>M. scabrinodis</i>	2/2	0/0	0/0	0/0	1/1	9/9
TOTAL	30/28	19/12	9/13	9/11	14/14	132/135
SLAVEMAKER SPECIES	0.0-.166	.167-.333	.334-.500	.501-.666	.667-.833	.834-1.0
<i>Harpagoxenus americanus</i>	4/4	3/2	1/1	1/1	1/1	9/10

sex (Talbot, 1972). Scherba (1961) censused alates of 107 colonies of *F. opaciventris* and found 93 that produced only one sex. Male or female colonies are quite common in *F. subintegra* (Talbot and Kennedy, 1940). In *F. rufa*, unisexual colonies are widely found and common (Marikovsky, 1961). Highly sexually biased nests were found in 12 *Formica* spp. in Finland (Pamilo and Rosengren, 1983). Unisexual colonies have also been found in *F. fusca*, *F. neorufibarbis*, and *Tapinoma sessile* (Kannowski, 1959), *Polyergus breviceps* (Kannowski, 1963) and *L. niger* (pers. observ.).

Evidence on mating capacities of ants have indicated that males might be severely restricted in the number of times they can

mate. This limitation implied that under LMC conditions one might expect roughly equal numbers of males and females. Despite a cumulative average MFRE (male frequency) near 0.5, however, in monogynous species only 23 per cent of all colonies had $0.333 \leq \text{MFRE} \leq 0.667$ (see Table 4). Of the 426 colonies examined, 67 (16%) produced females at numerical ratios greater than 10:1. Of the 22 species examined, 14 had colonies that displayed such an extreme female bias. With singly-mating males, the frequent occurrence of extremely numerically biased female broods is inconsistent with the predicted consequence of LMC.

All-male colonies are certainly not

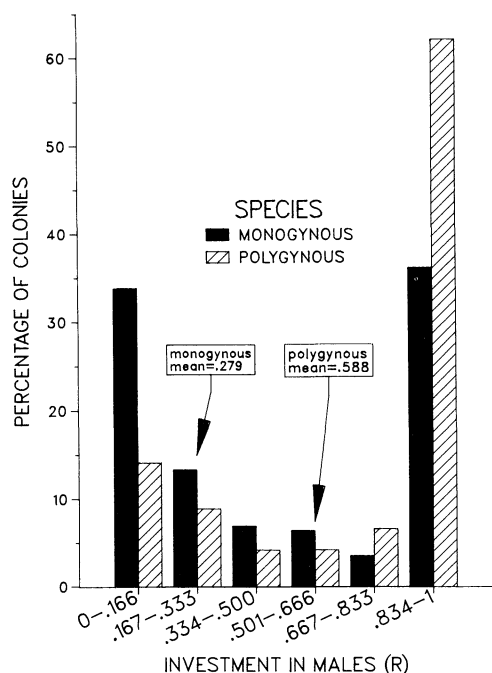


FIG 4. THE PROPORTION OF INVESTMENT IN MALES (R) BY INDIVIDUAL COLONIES

Notice the bimodality in both groups. *Tetramorium caespitum* is the only species that is obviously not bimodal (see Table 4), and so data from this species are not included in this figure.

predicted by LMC, whereas actually 27 per cent (115/426) were found with males only. A possible explanation for these male colonies is that the queen had died or had run out of sperm, so that only male-producing eggs were laid. In those unisexually male monogynous colonies, however, for which data are available, 94 per cent (75/80) also had worker (i.e., diploid) larvae or pupae. This indicates that although reproductives of both sexes could have been produced, only males in fact were.

The prevalence of extremely sexually biased colonies reduces the probability of within-nest mating. This situation is at odds with Taylor and Bulmer's (1980) model, which requires a high degree of within-nest mating if the observed ratios are to be predicted as a consequence of LMC.

Although the LMC hypothesis predicts no specific investment ratio, it does imply that most colonies capable of producing both

sexes should produce similar sex ratios. The bimodal patterns for investment and the numerical ratios found are inconsistent with LMC. Because with LMC, mating takes place within a restricted group, any deviations from the investment equilibrium would be penalized. To produce mostly one sex will lose more when that sex is over-abundant than can be gained when the other sex is over-abundant. This is because in finite populations a single-sex brood will move the sex ratio of the population back towards the equilibrium when the opposite sex is in excess and will thereby reduce its advantage. A single-sex brood of the sex in general excess will move the population away from the equilibrium and thus increase its disadvantage (Verner, 1965; Taylor and Sauer, 1980).

Other investigators (Alexander and Sherman, 1977; Darling, 1978; Herbers, 1979) have felt that the high number of sexual specialists existing is inconsistent with GRH. This need not be true for what GRH predicts is a population mean and not necessarily the condition of any individual colony. Sex ratio homeostasis, or selection for individual broods or colonies, that would split investment between the sexes at the equilibrium ratio is only significantly favored when the interbreeding population is quite small (Taylor and Sauer, 1980). When populations are sufficiently large that any individual brood will fail to alter the population's sex ratio, every investment strategy, from total male to total female bias, is equally fit (Williams, 1979). With allele frequency simulations, Pamilo (1982a) has predicted that single-sex broods can be expected under conditions of worker control where there is some worker-queen conflict. Hence GRH cannot be considered to be inconsistent with the data simply because a very few colonies produce exactly the equilibrium population investment ratio.

Sexual specialization might be favored and be increased by factors in addition to the population processes described above. Colonies that specialize in males or in females decrease the possibility of inbreeding in their offspring. Also, males and females, being so different in size and function, may require different methods of rearing. Single-sex broods might reduce the number of mistakes made by the workers (e.g., in treating a female larva as a male).

Discussion

Trivers and Hare's predictions are remarkably accurate, in particular regarding the investment in males on the part of so-called monogynous species. A number of factors, mentioned earlier, may have suggested a lessened female bias. These will now be examined in more detail. First, monogyny and polygyny are perhaps not distinct categories but only endpoints of a continuum. That is, every species listed as monogynous in Table 3 may indeed have some fraction of its population forming polygynous colonies. If so, might it not be expected that the average for the population would be a weighted average of the equilibrium sex ratios for polygyny and monogynous colonies? This reasoning is perhaps not accurate. Let us imagine an individual monogynous colony (with a fertile queen) in which the workers control the investment in sexuals and do not lay eggs themselves. These workers are at an investment ratio equilibrium only in a population with an average of $\bar{R} = 0.25$. Suppose there are also polygynous colonies that produce males at $R > 0.25$ (R = investment frequency in an individual colony), and hence shift the population's average to $\bar{R} > 0.25$. At this point, what would be the workers' fitness-maximizing strategy in the monogynous colony? Not to produce at $R = 0.25$, but instead to further increase their female bias so as to take advantage of the excess males in the population as a whole. In fact, the fittest strategy would be to produce nothing but females until $\bar{R}$ returns to 0.25 again! For the same reason, those colonies that favor more production of males because of polygyny or worker laying should produce nothing but males ($R = 1$) as long as the population's average is more female-biased than their own equilibrium value. This diversity could result in a population of sexually specialized colonies. However, unless the polygynous colonies produce a substantial proportion of the total population investment in sexuals, the population average might not be significantly shifted from the monogynous equilibrium of $\bar{R} = 0.25$. For instance, 10 per cent of polygynous colonies in a generally monogynous species may not translate into a 10 per cent shift (or even in any shift at all) toward the wholly polyg-

ynous equilibrium. Specialization in females on the part of monogynous colonies might compensate for any minor perturbations away from the predicted equilibrium.

The production of males by workers increases the degree of relatedness between workers and the average male in monogynous colonies. By GRH considerations, this relationship should reduce the female bias exhibited by the population. If all males are worker-produced, the worker equilibrium becomes $\bar{R} = 0.5$ or a 1:1 investment ratio (Oster, Eshel, and Cohen, 1977; Charnov, 1978; Benford, 1978). The data, however, do not reflect a significant shift away from the predictions based on non-laying workers of $\bar{R} = 0.25$. This fact seems to suggest that worker-produced males may be rare in healthy, queen-right colonies. The evidence tends to support this view. Even though workers do lay eggs in many ant species, it appears that in most of them these offspring are not raised to adulthood (Wilson, 1971; Crozier, 1974; Oster and Wilson, 1978; Pamilo and Rosengren, 1983). Oster and Wilson (1978) have shown that, as a general case, one should expect either the queen or the workers totally to dominate male production. In ants, mixed male parentage may be realistically expected only under a certain range of expected loss in the colony's foraging efficiency because of workers' commitment to laying.

Although it appears that workers do not lay significant numbers of viable male-producing eggs when healthy queens are present, they might do so in colonies in which the queen had died. That is, egg-laying by workers might be selectively advantageous when the queen is absent. Taylor (1981) derived formulas that predict individual colony and population investment equilibria under conditions where some percentage of colonies are restricted to producing only males. He assumed queen control of the investment ratio. If, however, one assumes worker control and follows Taylor's method of derivation, the equilibrium investment in males of a queen-right colony is:

$$R = (1/4) - (3\beta/8) \quad (1)$$

and the population investment is:

$$\bar{R} = (2 + 5\beta) / (8 + 8\beta), \text{ or} \quad (2)$$

$$\bar{R} = \beta / (1 + \beta), \text{ when } \beta \geq \frac{2}{3} \quad (3)$$

where β is the ratio of worker-produced male biomass over the total biomass of queen-produced sexuals. As can be seen from Eq. (2), the proportion of worker-produced males has to be quite large to shift the predicted mean substantially. From the data, only 6.2 per cent of unisexual male colonies appeared to have had no option for raising female sexuals (as inferred from the presence or absence of diploid worker larvae). It follows that colonies choosing to produce only males cannot be explained as a result of their lack of potential female sexuals. As a general phenomenon, workers producing only males to make the best of a bad situation seems to occur too infrequently to shift equilibrium values noticeably.

Sex ratio compensation may occur in *Rhytidoponera* species. In *R. confusa* an interbreeding population of sexuals is produced by two types of colonies: Type A, in which a queen produces both males and females; and Type B, in which the workers produce many males and a few female sexuals. Ward (1983) proposed that Type A colonies are overinvesting in females ($R < 0.25$), as a compensation for Type B colonies in the population. He found, for 80 Type A colonies in 10 populations, an overall $\bar{R}$ of 0.161. From Ward's data, the overall ratio of worker-produced males to queen-produced sexuals is $\beta = 0.262$. From Eq. (1), this ratio predicts that Type A colonies should invest at $R = 0.152$, a value very close to that observed. The population investment from all colonies is $\bar{R} = 0.354$, and the prediction from Eq. (2) is $\bar{R} = 0.328$. Both population values underestimate female investment because they do not include Type B colonies' investment in female function by means of forming new colonies by budding (Ward, 1983). Since this process adds few females to the pool of available mates, however, its effects should be minimal upon the foregoing predictions of investment ratio in Type A colonies.

It appears that the simplifying assumptions (a) of a dichotomous sorting of species into monogynous or polygynous, and (b) of the total production of all sexuals by the queen are generally justifiable for the Formicidae. One must use caution, however, in making these assumptions for all ant species. Some exceptions must certainly be expected.

As an example, there seems good evidence that in *Apterostigma dentigerum* perhaps over 40 per cent of the males are worker-produced (Forsyth, 1981). It is interesting that this species also shows a considerably reduced female bias ($\bar{R} = 0.514$), as would be predicted from worker-laying (Oster, Eshel, and Cohen, 1977; Charnov, 1978; Benford, 1978; Taylor, 1981). Also because adult colonies tend to be small (18 to 117 workers), some degree of the queen's control over the sex ratio is possible (Forsyth, 1981; Taylor, 1981).

There is also evidence for worker-produced males in *Myrmica* species (Brian, 1969; Brian, Jones, and Wardlaw, 1981; Elmes and Wardlaw, 1981). In this genus, often considerably more male-biased investment ratios are observed than are predicted by GRH when no worker-laying is assumed (see Table 1).

DETERMINATION OF SEX ALLOCATION WITHIN COLONIES

It is apparent from the data (see Fig. 4) that most colonies specialize in producing either heavily female-biased or male-biased sexual broods. A question remains as to the proximate means whereby the bias within any given colony is determined. Male specialization could be the only option available to colonies with no queen or queens without sperm, but as shown earlier this is a likely explanation for only a small fraction of male-specialist colonies. Male and female specialization could be, as discussed in the previous section, a pattern resulting when colonies of the same species have different social structures acting to maximize their individual fitness. For instance, polygynous colonies might favor males, whereas monogynous colonies might favor females. While this is a potent explanation for specialization, it may explain the behavior of individual colonies only in part. If one assumes that most colonies of a species have a similar social structure (e.g., monogyny), then some or all of the colonies will be selected to increase investment in males until the population's average approaches a 3:1 female bias. The investment ratios in these colonies may be determined in one of several ways.

One process that would work for all colony types would be to monitor the ratio of sexes in the population and then change the sex ra-

tio to maximize fitness. This seems, however, too complex an informational process to be workable in an ant society. Indeed, Herbers (1979) found no support for a similar hypothesis of information-sharing among the colonies in a population. She concluded that there was no stable equilibrium and that most colonies may be more or less random in the ratio of investment in the sexes.

The sex-investment ratio could be determined as a result of a balanced genetic polymorphism. The workers might be genetically predisposed to raising only female or only male sexuals. In that case, colonies would throughout their reproductive careers produce predominantly one sex. Frequency-dependent selection on these genes would produce a population average of $\bar{R} = 0.25$.

Alternatively, investment strategy could be determined facultatively in response to environmental conditions or to colony age and size. Elmes and Wardlaw (1982b) showed that production of sexuals is related to having a good nutritional state and hypothesized that the production of females is correlated with nest insolation. Also, colonies that are young, small, or that experience a poor foraging season may specialize in a particular sex (see Brian, Clarke, and Jones, 1981 for a numerical model predicting male broods in poor years). Herbers (1984) found that female bias was positively correlated to colony size.

There may be inferential support for the hypothesis of response to environmental conditions. Suppose that specialization in males or females is facultative, such that when a large amount of resources can be devoted to sexual broods, females are produced. Under poorer conditions, females become workers and the sexual brood is male-biased. Such facultative behavior ought to be reflected in the individual colony data. Colonies with a large amount of resource devoted to sexuals (i.e., producing many alates) should be more female-biased than those that had resources for only a few alates.

When the proportion of resources invested in males (R) is compared with the total amount invested in sexuals, in 29 species, 6 of them show a negative correlation with a significance level of $p < 0.05$ and an additional 6 species have $p < 0.13$ (Table 5). Moreover, although most species do not ex-

TABLE 5
Pearson correlation coefficients, r , between proportion of resources allocated to males (R) and the total amount invested in both sexes by individual colonies.

N equals the number of colonies examined and p is the significance level of the coefficient ($* = p > 0.15$). $R(25\%)$ = mean investment in males in the top 25 per cent of colonies as ranked by total weight of all sexuals. *Leptothorax longispinosus* correlations based only on data from Headley (1943).

MONOGYNOUS SPECIES	N	r	p	R(25%)
<i>Aphaenogaster rudis</i>	14	-.6133	.019	.165
<i>A. treatae</i>	12	-.8029	.001	.089
<i>Atta bisphaerica</i>	5	-.8338	.068	.186
<i>A. laevigata</i>	6	-.6880	.123	.174
<i>A. sexdens</i>	7	+.1785	*	—
<i>Camponotus ferrugineus</i>	6	-.2551	*	.082
<i>C. pennsylvanicus</i>	4	-.6656	*	.087
<i>Formica fusca</i>	18	-.2892	*	.382
<i>F. pallidefulva nitidiventris</i>	19	-.4171	.075	.001
<i>Lasius flavus</i>	10	-.6073	.061	.017
<i>Leptothorax curvispinosus</i>	10	-.3312	*	.155
<i>L. longispinosus</i>	13	-.5431	.054	.029
<i>Myrmica ruginodis</i> (macrogyne)	32	-.5803	.001	.256
<i>M. schencki</i>	10	-.1695	*	.089
<i>M. sulcinodis</i>	104	-.2683	.006	.482
<i>Pogonomyrmex montanus</i>	35	+.0358	*	—
<i>F. ruginodis</i>	4	-.8113	*	.315
<i>F. subnitidus</i>	7	-.7380	.054	.302
<i>Frenolepis imparis</i>	12	-.1309	*	.211
<i>Stenamma brevicorne</i>	8	-.3710	*	.334
<i>S. diecki</i>	10	-.3091	*	.202
<i>Tetramorium caespitum</i>	80	-.0027	*	.405
POLYGYNOUS SPECIES	N	r	p	
<i>Formica obscuripes</i>	44	-.1744	*	
<i>F. pallidefulva incerta</i>	12	+.1583	*	
<i>Myrmica rubra</i>	11	-.3699	*	
<i>M. ruginodis</i> (microgyne)	8	+.0515	*	
<i>M. sabuleti</i>	126	-.2069	.020	
<i>M. scabrinodis</i>	12	-.9541	.001	
SLAVERMAKING SPECIES	N	r	p	
<i>Harpagoxenus americanus</i>	19	+.0502	*	

hibit strong correlations, 24 of the 29 do have negative values of the Pearson correlation coefficient. This indicates a significant trend across species (sign test; $t = 3.528$, $p < 0.001$). These results also argue against the genetic predisposition hypothesis, as that would predict no correlation between sex ratio and amount invested. Nor does it support Herbers' (1979) conclusion that sex ratio patterns will generally be unordered.

When resources are scarce, males might still be raised while females are channelled into becoming workers. However, when resources are plentiful do colonies specialize in females? To answer this, I examined the investment ratios in the top 25 per cent (as

ranked by total weight of all sexuals) of colonies for the 20 species in the monogynous group that showed a negative correlation. When less than 8 colonies were available, I used the top two. In this group, the mean investment in males was $\bar{R} = 0.175$, a value that translates to a 4.71:1 female bias (see Table 5). This average was significantly less than the predicted mean of $\bar{R} = 0.25$ on the basis of a 3:1 female bias ($t = 2.126$, $df = 19$, $p < 0.025$, all data arcsine transformed). In the 10 species with correlation coefficients of significance level $p < 0.13$, the average is $\bar{R} = 0.135$ (a female bias of 6.41:1), significantly less than $\bar{R} = 0.25$ ($t = 2.005$, $df = 9$, $p < 0.05$). In polygynous species, colonies with abundant resources may also over-produce females, but that is difficult to test on account of smaller sample sizes and no single predicted mean investment because the degree of relatedness within the average colony may vary between species. The working hypothesis is only that polygynous species invest between $0.5 \geq \bar{R} > 0.25$. I believe the sum of the data strongly suggests that ants facultatively switch their investment ratios in response to resource abundance.

Herbers (1984) found that investment in males was negatively correlated with colony size, as measured by number of workers in *Leptothorax longispinosus*. She suggested that this relation held because, as worker numbers increased, they were more likely to win in worker-queen conflicts and to produce investments closer to their equilibrium. However, she found this relationship in both monogynous and polygynous colonies. While that might be expected with monogyny, worker and queen equilibria converge under polygyny. One would therefore predict no effect on investment ratios in polygynous colonies as number of workers increased. Another possible explanation is that colony, or ergonomic, efficiency increases with size of colony (Oster and Wilson, 1978). If larger colonies hence tend to gather more food, colony size might affect investment ratios more through increased foraging efficiency than by worker-queen conflict mechanisms.

Boomsma, Van der Lee, and Van der Have (1982) found inferential support for the idea that resource stress affects sex ratios. They compared the investment ratios of *Lasius niger*

colonies that were food-limited through competition with *L. flavus* with those in an area where *L. flavus* was absent. The colonies in the area of intense competition produced significantly less female-biased investment ratios, and the competition appeared to affect female production much more than male production. Pontin (1961) found similar effects in *L. flavus* colonies due to competition with *L. niger*. Brian (1979) found more female production in optimal habitats than in marginal ones for *L. alienus* and *Tetramorium caespitum*.

Further studies of population and individual colony investment ratios, using game theory and evolutionary stable strategy modelling as described by Maynard Smith (1982) and by Charnov (1982), may prove enlightening. Obviously no single, simple evolutionary strategy (e.g., produce males at $R = 0.25$ for all monogynous colonies) is at work. Some colonies that have no fertile queens or experience a poor foraging year may have to follow a conditional strategy in which if any sexuals can be raised, they are males. In response, colonies with large resource bases seem to choose a tactic of over-investing in females. An evolutionarily stable state within a population might then be evolved as a response to the local ecological conditions. The amount of resource stress within the environment may select for tolerance levels such that the switch-over from male to female production produces an overall 3:1 female population bias. It would be interesting to manipulate colonies experimentally to see if a resource-mediated switch point from male bias to female bias actually occurs. Facultative switches in the sex ratio of offspring have been demonstrated in other species (Charnov and Bull, 1977; Bull 1980; Vogt and Bull, 1984).

CONCLUSIONS

In predicting sex investment allocation ratios in ants, Trivers and Hare's (1976) genetic relatedness hypothesis is remarkably robust. GRH gives explanations why the investment ratio is affected by monogyny or polygyny both across and within species and also explains the effects of non-conspecific brood care. A number of species were examined to test these predictions, and they were strongly

supported in all cases. The observed extremely high variance in investment ratios between colonies is not contrary to GRH predictions. Selection appears to have produced a balance of sexual specialist colonies such that a population approximates the investment equilibrium of the dominant social type.

The GRH may not predict particularly accurately the sex ratio within a single colony. Local conditions may vary investment between colonies, or produce within a single colony ratios that can either be variable from year to year (Herbers, 1979) or stable (Pamilo and Rosengren, 1983). Proximate factors such as food availability, nest insolation (Elmes and Wardlaw, 1982b), or polydomy (Pamilo and Rosengren, 1983) may be much more descriptive. On a population or ultimate level, however the degree of genetic relatedness must be seriously considered as a factor in producing the observed sex ratios, at least in the Formicidae and perhaps in all eusocial Hymenoptera.

The local mate competition hypothesis, as proposed by Alexander and Sherman (1977), fails to explain adequately the patterns of sexual investment in ants. The numbers of males found, the breeding biology, the investment ratios in slavemaking and parasitic species, and the high proportion of sexual specialist colonies are all inconsistent with LMC predictions. Although local mate competition may affect some species under certain conditions, it cannot be a broad explanation of ant sex allocation, as it appears GRH, the alternative hypothesis, can be.

The hypothesis that males have only one or a few matings, if correct, generates interesting speculation. Queens, by living for a number of years, could utilize sperm of several males. This possibility means that the maximum number of offspring to which an individual female contributes genes could be

much greater than the maximum number of offspring of an individual male. There would then be a larger variance in the reproductive success within the female sex than in the male sex. This is the opposite of what is normally assumed to hold true for most species (Bateman, 1948; Wade, 1979; Wade and Arnold, 1980). In ants, then, whenever numerical sex ratios are close to 1:1, males (i.e., sperm) could be a limiting resource in reproductive output, and perhaps sexual behavior roles in ants might be to some extent reversed.

Most individual colonies in many species specialize in producing either extremely male-biased or female-biased sexual broods. This may be a mixed evolutionary strategy, with perhaps both conditional and facultative tactics (Charnov, 1982). When resources are poor or the queen is dead or without sperm, then males are produced; when resources are good and the queen healthy, females. The interplay between these tactics, because of differences in social structure and local conditions, may go far to explain both the investment strategy of individual colonies and population values that appear to be determined by considerations of genetic relatedness.

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