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## Sex Ratio and Sexual Dimorphism in *Formica Exsectoides*, the Allegheny Mound Ant (Hymenoptera: Formicidae)

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SEX RATIO AND SEXUAL DIMORPHISM IN *FORMICA EXSECTOIDES*,  
THE ALLEGHENY MOUND ANT (HYMENOPTERA: FORMICIDAE)H. C. Rowe<sup>1, 2</sup> and C. M. Bristow<sup>1</sup>

## ABSTRACT

We excavated 66 mounds from 6 populations of *Formica exsectoides* in Michigan jack pine, collecting sexual caste pupae for sex ratio estimates and measurement of dimorphism. Reproductive caste brood was present in only 37 of the 66 mounds, and presence of reproductive caste brood was associated with larger mound surface area. Females were heavier than males, but did not differ from males in energy density. Sexes did not differ in timing or rate of development. Sex ratio estimates based on individual mounds ranged from 1.0 (all male) to 0.08 (female-biased). Four of the six study populations were strongly male-biased, while sex ratio estimates for the remaining populations did not differ from equal investment. While this interpopulation variation may be caused by genetic factors, the equal investment populations were located in or near patches of clear-cut forest, suggesting that environmental impacts should be investigated.

The conspicuous nests of *Formica exsectoides* Forel, the Allegheny mound ant, are a visual echo of its great ecological importance. Ranging from Ontario to Tennessee and northern Georgia, *F. exsectoides* form dense populations along forest edges and in persistent grassy clearings (Creighton 1950). In the Great Lakes region, these ants are an important feature in jack pine forests (Bristow et al. 1992). While extensive descriptions of the physical structure, placement, and orientation of mounds exist (McCook 1877, Andrews 1926, Andrews 1929, Cory and Haviland 1938, Haviland 1948, Dimmick 1951), information on the biology of the builders is more limited.

High-density populations of *F. exsectoides* can dominate the jack pine (*Pinus banksiana*) landscape in northern and central Michigan. As both ground-level and arboreal predators and participants in mutualistic tending relationships with multiple groups of phloem-feeding homopterans, *F. exsectoides* may play a vital role in the structure and linkage of ground-dwelling and arboreal communities (Bishop 1998).

*F. exsectoides* possesses an unusual suite of reproductive and behavioral traits. New colonies are founded through temporary social parasitism of *Formica fusca* L., in which *F. exsectoides* queens enter an established *F. fusca* colony and replace its queen (Wheeler 1933, Starr 1979). *F. exsectoides* colonies are polygynous (possessing multiple queens) (Bristow et al. 1992).

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Colonies may expand through nest budding; the departure of a queen or queens and a group of workers to establish a new mound (Franks and Hölldobler 1987). This process does not entail complete separation from the "parent" mound, and thus creates colonies that are polydomous (occupying multiple nests) (Oster and Wilson 1978). Finally, *F. exsectoides* colonies show an unusual lack of intercolony aggression. Greater knowledge of their reproductive biology is essential for understanding how these ants colonize and expand within habitats.

Reproduction, and sex ratio in particular, is of great interest in the study of ants and other social Hymenoptera. Hymenoptera possess a haplo-diploid system of sex determination, which may lead to increased relatedness between diploid female offspring and decreased relatedness between female offspring and their haploid brothers. In Hymenoptera, sex ratio often varies from the equal investment predicted by Fisher (1939), and may be influenced by asymmetric relatedness among siblings, environmental factors, and genetically and environmentally influenced variation in sexual dimorphism.

The extent of sexual dimorphism in weight, energy content, and metabolic costs affects sex ratio and is a key determinant of how investment should be estimated (Boomsma et al. 1995). Simply counting the number of males and the number of females produced by a colony will only reflect true investment if males require the same input as females. While weight is most commonly used as a surrogate measurement for investment, Boomsma (1989) found that this led to an overestimate of colony investment in females, by overlooking the higher respiration rate of males. Boomsma's proposed correction is now widely employed, but few studies investigate other possible differences between males and females, such as energy density, which might obscure true investment ratios.

The abundance of variation in hymenopteran sexual investment has fostered the growth and testing of a rich body of evolutionary theory concerning kin selection, parent-offspring conflict and the evolution of sociality (Hamilton 1964, Trivers and Hare 1976, Charnov 1982, Nonacs 1986, Crozier and Pamilo 1996). The unusual biology of *F. exsectoides* makes it potentially informative to this theory (Oster and Wilson 1978, Starr 1979, Bourke and Franks 1995), but useful tests are impossible without prior information on reproductive biology and sex ratio.

The purpose of this study is to describe sex ratio in *F. exsectoides*. This description necessarily includes measurement of sexual dimorphism in both weight and energy content, interpopulation variation in sex ratio and dimorphism, and potentially correlated colony characteristics such as mound size and spacing. These data are an essential foundation for further study of this species. While such data may be the basis for predictions in testing sex ratio theory, knowledge of *F. exsectoides* reproduction will also improve understanding of this ecologically complex ant species and be of broad use to researchers interested in the biology and conservation of other members of the jack pine community.

## METHODS AND MATERIALS

**Site locations.** Study sites were located in Oscoda, Crawford, and Roscommon counties, in the northern lower peninsula of Michigan. Because all sites were noncontiguous and located at least 1 km apart, we assumed discrete populations. Vegetation consisted predominantly of jack pine with interspersed red pine (*Pinus resinosa*), northern pin oak (*Quercus ellipsoidalis*), and cherry (*Prunus* spp.). Understorey vegetation consisted primar-

ily of blueberry (*Vaccinium angustifolium*), sand cherry (*Prunus pumila*), bracken fern (*Pteridium* spp.) and grasses (*Carex* spp.). All sites were located in 50 to 70 year-old stands, with the exception of site 4, which had been recently clear-cut.

**Brood collection and measurement.** Partial excavations of 66 mounds from 6 sites were performed from 18 July to 26 July 1996. For each mound, a comparative index of mound surface area (longest slope  $\times$  shortest slope) and the distance to the nearest neighboring mound were recorded. Presence or absence of reproductive caste brood was determined by excavating the mound to approximately 0.5 m below ground level (or until reproductive caste pupae were found). Reproductive caste pupae are easily distinguished from worker pupae by size and coloration.

Samples of 30–90 reproductive caste pupae were collected from mounds found to contain reproductive caste brood. Pupae were dried and weighed. Sex was determined visually after removing the pupal case. Some pupae had not developed enough for sex to be distinguishable by morphology; these were scored as “undeveloped” and excluded from further analysis. Stage of pupal development was scored from 0 (undeveloped) to 3 (fully developed, pigmented, ready to eclose). A few adults had partially emerged—these were given a score of 3.5. Analysis of covariance was used to analyze pupal dry weights, with sex as the primary analysis variable and stage of development as the covariate (PROC ANCOVA, SAS Systems Inc., 1990).

**Energy content.** Caloric densities of pupae were measured using a semi-micro calorimeter (Parr Instrument Company, Moline, IL). Heat of combustion in calories/g ( $H_c$ ) was calculated by the equation:

$$H_c = ((B \times \Delta T) - ((f_1 - f_2) \times 1400)) / \text{sample weight}$$

where B is a caloric constant, calculated through calibration with benzoic acid,  $\Delta T$  is the change in temperature occurring during combustion, and  $(f_1 - f_2) \times 1400$  is a correction factor accounting for the amount of fuse wire used to ignite the sample.

Since measurement accuracy declines sharply in samples below 0.01g weight (Parr 1991), 3–5 individuals of each sex were measured together. At least three samples from each site were analyzed to determine energy content of males; it was often not possible to analyze three (or any) samples of females, as fewer females were available. The data were analyzed using a nested analysis of variance in the following hierarchy: days (mounds (sex)). The variable “days” accounts for variation in calorimeter performance during the analysis.

**Calculation of sex ratio.** Sex ratio was estimated numerically (number of males/total number of pupae) and by dry weight (dry weight of males/ dry weight of total sample). As pupae within samples were usually of the same developmental stage, weights were not corrected for developmental stage. Numerical and weight-based sex ratio estimates were compared to each other using a paired t-test. As male ants have been shown to have higher respiration rates than females (MacKay 1985, Boomsma 1989), weight-based sex ratios were corrected for differences in metabolic rate using Boomsma’s (1989) energetic cost ratio. These corrected ratios were compared between mounds and between sites using a nested analysis of variance. Boomsma-corrected sex ratios were also correlated to mound surface area and distance to nearest neighbor using PROC CORR (SAS Systems Inc., 1990).

Table 1. *Formica exsectoides* sampling data and sex ratios, by site.  $n$  = total number of pupae collected,  $n_r$  = number of pupae used to calculate sex ratios,  $M_n$  = numerical proportion of males in total sample,  $M_w$  = proportion of male investment by dry weight,  $M_{bw}$  = Boomsma (1989) cost ratio. Boomsma cost ratio is generated by correcting dry weight ratios with Boomsma's (1989) energetic cost ratio: (weight males/weight total)<sup>0.7</sup>.

Site	Mounds		$n$	$n_r$	$M_n$	$M_w$	$M_{bw}$
	Excavated	Sampled					
1	9	7	347	306	0.791	0.768	0.831
2	13	8	389	336	0.902	0.882	0.916
3	14	7	382	350	0.820	0.781	0.841
4	5	2	66	64	0.453	0.384	0.512
5	20	6	232	222	0.658	0.605	0.704
6	5	3	114	98	0.959	0.952	0.966

## RESULTS

**Mound measurements and collection of brood.** Reproductive pupae were only found in 37 of 66 partially excavated mounds. Of these 37, only 33 mounds contained sufficient pupae (25–30) for sex ratio sampling. Table 1 provides a summary of excavations, sampling, and sex ratios for each site. Sites 4 and 6 contained relatively few mounds. A total of 1530 pupae were collected. Twenty pupae were removed from the analyses due to damage that caused inaccuracy in weight measurements or uncertainty about sex. Of the remaining sample, 134 pupae had not developed sufficiently for sex to be morphologically distinguishable; these were classified as “undeveloped”, and are subtracted from the total pupae sampled to provide the value  $n_r$  (number of pupae for ratios) shown in Table 1.

Mound surface area ranged from 0.9 m<sup>2</sup> to 12.5 m<sup>2</sup>. Distance to nearest neighboring mound ranged from 1 m to 51 m. Only active/inhabited mounds were counted as “neighbors”. The mean surface area index for mounds found to produce sexual brood was marginally greater than that for mounds that produced only worker brood ( $F = 3.84$ ,  $df_e = 46$ ,  $p = 0.0560$ ), but this relationship was variable among sites (Figure 1). Distance from nearest neighboring mound did not appear to be associated with production of sexual brood ( $F = 0.03$ ,  $df_e = 46$ ,  $p = 0.8662$ ) (Figure 2).

**Weight and development.** Females were heavier than males ( $F = 160$ ,  $df_e = 1353$ ,  $p < 0.0001$ ). The mean female weight (least squares mean, corrected for developmental stage using ANCOVA) across all sites was 0.0101 (stderr = 0.00007;  $n = 276$ ). The mean male weight across sites was 0.0081 (stderr = 0.00004;  $n = 1100$ ).

While significant differences in pupal weights of both sexes existed among sites, variation in weights was also found among mounds within sites. Male and female pupal dry weights are shown in Figure 3.

Some of this weight variation was linked to variation in stage of pupal development. Significant negative regression relationships existed between development stage and pupal dry weight for both sexes (Figure 3). The regression slopes were similar between sexes, but development stage explained less variation in male weight ( $r^2 = 0.1787$ ) than in females ( $r^2 = 0.2934$ ), due to the presence of outliers in the male weight data. Mean stage of pupal development was not different among mounds or among sites.

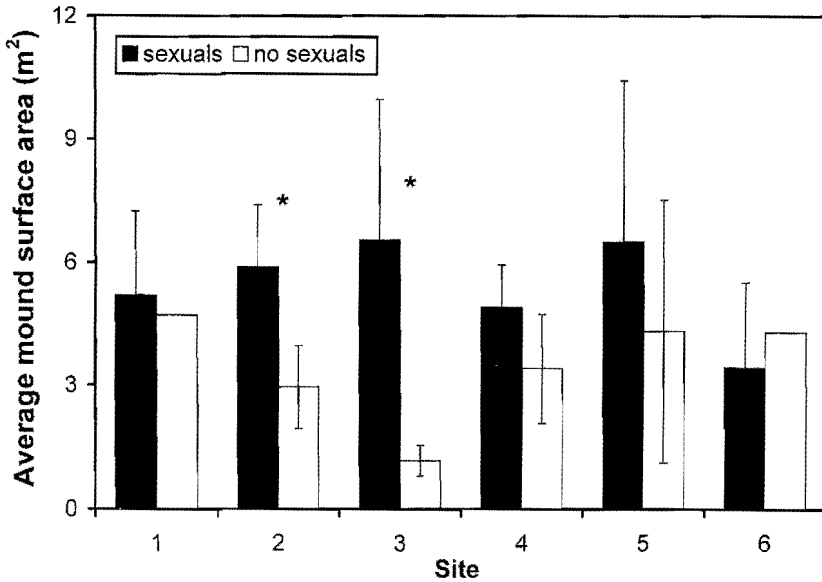


Figure 1. Comparative surface area measurements (m<sup>2</sup>) for *Formica exsectoides* mounds with and without reproductive caste brood. Comparative surface area was measured as (longest slope of the mound surface) × (shortest slope of the mound surface). Sampling data is reported in Table 1. Error bars represent one standard deviation.

**Energy Content.** There was no significant difference between energy density (corrected H<sub>c</sub>) of male and female pupae ( $F = 0.35$ ,  $df_e = 74$ ,  $p = 0.5576$ ) (Figure 4). The least-squares means of energy density for males was 5526.2 cal/g, and for females 5507.9 cal/g. The overall nested ANOVA model:  $H_c = \text{day}(\text{site}(\text{sex}))$  was not significant at  $p = 0.5001$  ( $F = 0.88$ ,  $df_e = 74$ ). As pupae could not be combusted individually, it was impossible to test for differences in caloric density among stages of development.

**Sex Ratios.** As males and females were not different in energy content, caloric content data could not be used to estimate sex ratio. Numerical and dry-weight estimates of sex ratio were statistically different ( $t = 5.64997$ ,  $df = 32$ ,  $p = 0.0001$ ). Due to the differences between male and female weights, using numbers of individuals to estimate sex ratio overestimated investment in males by an average of 2.8% compared to estimates based on weights. Whether this difference would be meaningful in a larger context depends largely on the precision of theoretical predictions tested. Applying Boomsma's (1989) correction increases the male bias to a greater extent than using the original numerical investment ratio. As sex ratio estimates based on dry weights seem more accurate in determining investment, and the Boomsma correction is accepted by convention, Boomsma-corrected weight ratios are discussed in the remainder of this article.

Sex ratios were predominantly male-biased, but ranged from all-male (1.0) to almost all-female (0.08). Although considerable variation in sex ratio

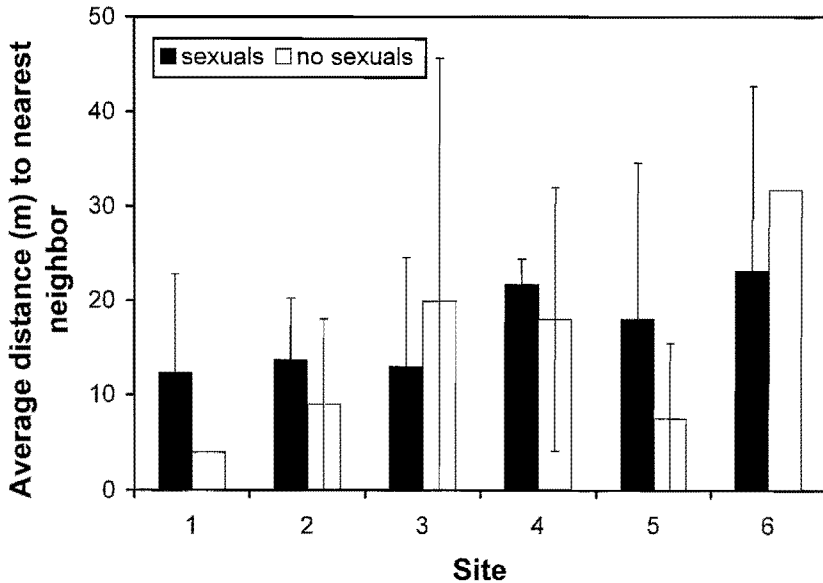


Figure 2. Average distance (m) to nearest neighboring mound for *F. exsectoides* mounds with and without reproductive caste brood. The number of mounds sampled at each site is reported in Table 1. Error bars represent one standard deviation.

was present within sites, polydomy of *F. exsectoides* colonies makes mound to mound comparisons questionable without further genetic information. Thus sex ratio estimates from all mounds within a site are treated as samples of a single population, and only comparisons between population averages were performed. Population mean numerical and weight-based sex ratios are shown in Table 1.

Analysis of variance showed differences in sex ratio among sites ( $F = 3.1$ ,  $df_e = 27$ ,  $p = 0.0245$ ) (Figure 5). Sites fell into two categories: male-biased (sites 1, 2, 3, & 6), and sites with sex ratios not differing from 50/50 or equal investment (sites 4 & 5). Sites 4 and 5 contained male-biased mounds, but these were balanced by female-biased mounds.

## DISCUSSION

**Mound measurements and collection of brood.** The relatively low percentage of *F. exsectoides* mounds containing reproductive brood may be explained in the context of a polydomous colony—one or a few mounds within the colony may contain all of the colony's sexual offspring. The environment in some mounds might be better suited for production (or pupation) of sexual offspring. Gain in efficiency of brood care might arise from clustering sexual brood in a few mounds, rather than scattering it among many. Alternatively,

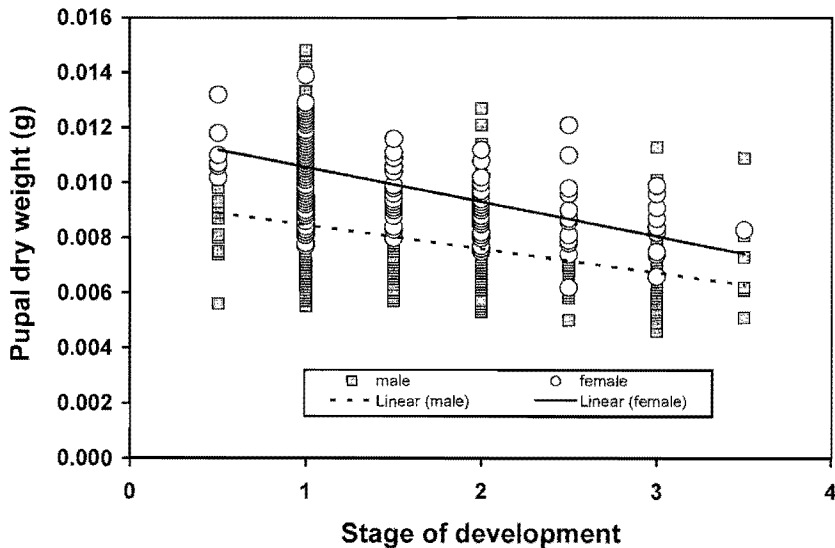


Figure 3. Dry weight (g) of male and female *F. exsectoides* sexual caste pupae. Developmental stages are based on pigmentation, sclerotization, and definition of adult features. These stages range from 0 (still larval, unable to determine sex by morphology) to 3.5 (partially emerged from cocoon). Regression slopes shown were significant at  $p < 0.0001$ .

a lack of production of sexual forms may reflect allocation to asexual colony expansion (budding). Budding should be a more successful method of expansion within habitats, since it does not depend on availability of *F. fusca* host nests. Alate sexual forms are usually vulnerable to predation during dispersal (Hölldobler and Wilson 1990), and may be an unnecessary investment in stable habitats.

While mound surface area is not a good surrogate for direct measures of worker population (Cory and Haviland 1938), or even mound volume (Bristow et al. 1992), the measurement has some value in comparisons between established mounds and newly-formed buds. As mound size increases over time (Andrews 1926, Haviland 1948), the tendency for mounds producing sexual brood to be larger in surface dimensions than mounds producing only workers may reflect differences in colony maturity (Figure 1). Measurements of distance to the nearest neighboring mound may be expected to reflect crowding, local competition for resources, and frequency of budding, all factors of potential influence on reproductive allocation within a mound. Current data do not show an effect of neighbor distance on reproduction (Figure 2).

**Weight and development.** Differences in pupal development within and between mounds may arise from environmental factors (mound temperature, placement of pupae within mound), colony factors (time of egg-laying, maternal effects, nutrition), or genetic factors influencing development time. The data obtained in this study give no indication that males and females



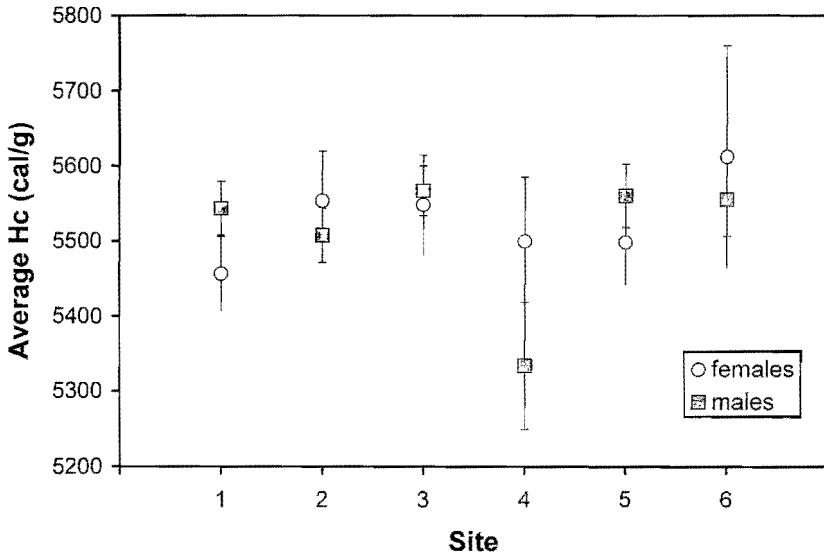


Figure 4. Energy density ( $H_c$ , measured as cal/g) of male and female *F. exsectoides* reproductive caste pupae. Error bars represent one standard deviation.

differ in development rates or emergence times (Figure 3). While sex of “undeveloped” pupae cannot be determined (inviting conjecture that differences in development time may obscure the true sex ratio), relatively equivalent proportions of males and females at each developmental stage lends support to the contention that “undeveloped” pupae represent a random assortment of males and females.

Weight data indicated significant dimorphism between males and females, but the difference between sexes was small relative to that shown by many ant species (Boomsma 1989, Crozier and Pamilo 1996). This is consistent with the founding biology of *F. exsectoides*—species with dependent (non-claustral) founding tactics, such as budding and social parasitism, require less investment per female. Founding biology also explains the lack of difference in male and female energy density, as females do not require large fat reserves for founding new colonies.

The sexual dimorphism in weight was partially masked by the presence of male weight outliers. These were usually males that were as heavy or heavier than females. These males were often also outliers with respect to appearance, possessing disproportionately large heads. The presence of these “heavy” males might indicate a dispersal polymorphism such as that described by Fortelius et al. (1987) and Agosti and Hauschteck-Jungen (1987) in *Formica exsecta* L., in which small males dispersed while larger males mated in the vicinity of the nest. The low frequency of these males among *F. exsectoides* sampled argues against that explanation. Alternatively, these males could be diploid. Nipson’s (1978) study, as well as the colony structure and mating behavior of *F. exsectoides*, suggests that significant inbreeding

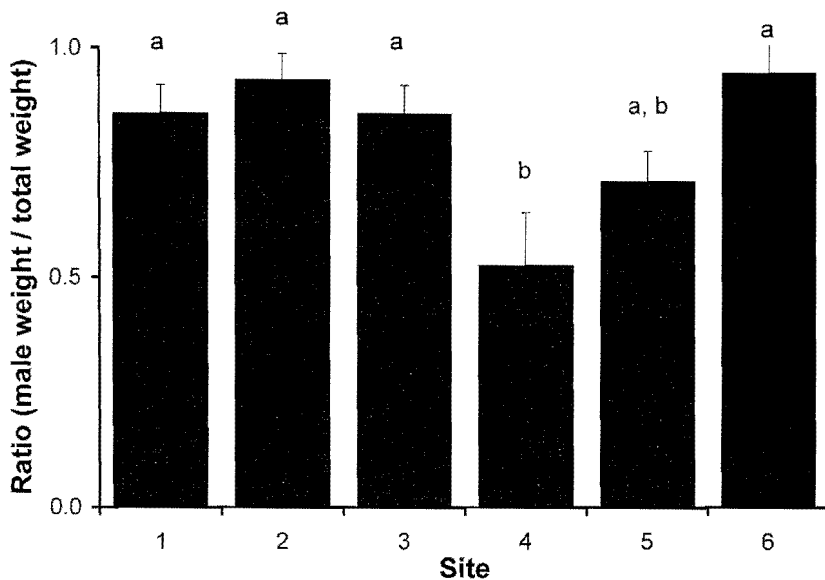


Figure 5. Sex ratio of *F. exsectoides* populations, based on dry weight measurements of sexual caste brood. Boomsma's (1989) correction for metabolic costs has been used. Each value represents the mean of mounds sampled from that site; sampling data are provided in Table 1. Error bars represent one standard deviation. Letters 'a' and 'b' are used to indicate statistically significant differences between populations.

may occur within populations. Inbreeding may lead to the production of diploid individuals homozygous at sex-determining loci—intended females who are morphologically male and reproductively dysfunctional (Crozier 1971, Pamilo et al. 1994). The presence of diploid males as a significant fraction of the reproductive brood produced would lead to overestimation of male investment, and should be investigated in the future.

**Sex Ratio.** The strong male bias in sex ratio displayed by *F. exsectoides* is surprising, as relatedness asymmetries in eusocial Hymenoptera are expected to result in worker preference for a female bias (Trivers and Hare 1976). The male bias observed is consistent with observed sex ratios for other ant species that display colony expansion through budding (Bourke and Franks 1995, Pamilo and Rosengren 1983). Unfortunately, budding is associated with a suite of characteristics, such as polygyny and polydomy that may equally influence sex ratio (Boomsma 1993). The extent of any or all of the above traits may be related to genetic, social, or environmental factors.

Our observation that sites located within (site 4) or near (site 5) recently clear-cut forests had sex ratios not different from 50/50, while all other sites had strongly male-biased sex ratios (Figure 5) suggests an environmental influence. Two environmental factors with strong potential effects on female investment are food and availability of nest sites. Food availability may contribute directly to sex ratio, either through developmental effects (lack of

food results in fewer sexuals, more workers (Deslippe and Savolainen 1995, Herbers and Banschbach 1998)) or by influencing reproductive allocation. The theory of local resource competition (Clark 1978) states that, in a resource and dispersal-limited environment, male production will be favored since female offspring will compete directly with the mother for resources. While this theory is not consistent with observations in this study (clear-cut areas may be expected to have reduced food resources), it is possible that differences in sex ratio among sites represent population-level strategies for coping with ecological conditions. The effect of environment on sex ratio may also be indirect. Herbers (1986, 1993) discusses the impact of ecological factors on queen number, which may affect sex ratio by altering the relatedness structure of the colony. Detailed comparisons between populations along a gradient of environmental conditions would be necessary to determine the existence of these strategies and the factors regulating them.

Understanding patterns of reproduction in *F. exsectoides* is an essential preliminary to understanding the population dynamics of this species and how those dynamics shape its relationship to the surrounding community. Factors that make sex ratio studies of *Formica exsectoides* difficult, such as polydomy, social parasitism, and specialization on transient habitats, increase the need to perform such studies, since understanding sex ratio and reproductive dynamics in only discrete, monogynous laboratory colonies gives an incomplete picture of the interaction of genetic and environmental factors in shaping reproductive strategy. Before integrating sex ratio studies in large-scale evolutionary analyses, researchers must understand the extent of variation present. This study indicates that intraspecific variation in sex ratio exists in *F. exsectoides*, whether due to environmental or genetic influences. As significant variation in sex ratio occurred between sites *within* a specific habitat (jack pine), whole species generalizations of sex ratio based on one or two studies will surely misrepresent true sex ratio dynamics of many ant species.

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