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SEX-BIASED SIZE VARIATION IN VELVET ANTS (HYMENOPTERA: MUTILLIDAE)

MARK DEYRUP

Archbold Biological Station

P.O. Box 2057

Lake Placid, FL 33852

and

DONALD MANLEY

Clemson University

Pee Dee Research and Education Center

P.O. Box 5809

Florence, SC 29502

ABSTRACT

The relative sizes of male and female Mutillidae were studied at the Archbold Biological Station in south-central Florida. Females are larger than males in *Dasymutilla pyrrius* (Fox), *Pseudomethoca sanbornii aetis* (Fox), and *P. oculata* (Banks). Males are larger than females in *Timulla d. dubitata* (Smith), *T. floridensis* (Blake), *Ephuta f. floridana* Schuster, *E. m. margueritae* Schuster, *E. s. slossonae* (Fox), *Dasymutilla archboldi* Schmidt and Mickel, and *Photomorphus paulus* (Bradley). There is no significant difference in *Dasymutilla asopus bexar* (Blake), *D. nigripes* (Fabricius), and *D. castor* (Blake). Sex-biased size variation may be associated with courtship behavior or host-seeking behavior.

RESUMEN

Se estudió el tamaño relativo de machos y hembras de Mutillidae en la Estación Biológica de Archbold en el centro-sur de la Florida. Las hembras son más grande que los machos en *Dasymutilla pyrrius* (Fox), *Pseudomethoca sanborinii aetis* (Fox), y *P. oculata* (Banks). Los machos son más grande que las hembras en *Timulla d. dubitata* (Smith), *T. floridensis* (Blake), *Euphata f. floridana* Schuster, *E. m. margueritae* Schuster, *E. s. slossonae* (Fox), *Dasymutilla archboldi* Schmidt y Mickel, y *Photomorphus paulus* (Bradley). No hay diferencia significante en *Dasymutilla asopus bexar*

(Blake), *D. nigripis* (Fabricius), y *D. castor* (Blake). Variaciones de tamaño parciales al sexo pudieran estar asociadas con el comportamiento de cortejo o la búsqueda de hospedero.

Among solitary parasitoid wasps, the size of the adult insect is limited by the size of the host consumed by the larva. The sex of the wasp is normally determined by whether the individual is haploid (male) or diploid (female) (Flanders 1946). A mated female can potentially determine the sex of an offspring by releasing or withholding stored sperm at the time of oviposition (Flanders 1946). Parasitoid wasps that attack larvae of varying sizes have the opportunity, if the wasp is able to gauge the size of the host, to allocate hosts to one sex or the other on the basis of size. Such sex-biased host allocation occurs in the braconid *Coeloides brunneri* Viereck (Ryan 1961), in the braconid *Heterospilus prosopidis* Viereck, and the pteromalid *Lariophagus distinguendus* (Foerster) (Charnov 1982), all of which tend to lay male eggs on small hosts and female eggs on large hosts.

Velvet ants (Mutillidae) are, in certain ways, particularly well suited for a survey of sex-correlated size variation in natural populations. All species for which hosts are known are solitary parasitoids that feed on fully grown host prepupae and pupae (Mickel 1928); continued host growth after the parasitoid has chosen the sex of her offspring does not complicate analysis. We assume that the larvae completely consume their hosts, as we know of no examples of solitary parasitoids that share a cell with a partially consumed host. There is obvious size variation in some species of velvet ants. At our study site, for example, female *Dasymutilla pyrrhus* (Fox) vary from 8.9 to 15.5 mm in length, and male *Timulla floridensis* (Blake) vary from 6.0 to 13.6 mm. Mickel (1928) showed that size variation in adult velvet ants is related to host size in the case of *Dasymutilla bioculata* (Cresson), whose bimodal size distribution (in both sexes) is correlated with the different sizes of its two host species. Preliminary surveys of collections of velvet ants from various sites indicated tendencies toward sex-biased size differences in some species, random size variation in other species, and little size variation in other species. Of particular interest was the relatively large size of males of a number of species. Velvet ants seem to offer an intriguing diversity in allocation of resources between the sexes.

Although museum collections give an indication of patterns in size variation, these collections do not make a good data base because many collectors preferentially capture large "fine" specimens. Moreover, the specimens in a normal collection do not reflect the consensus of size allocation by females of a population faced with the same spectrum of hosts. The range of host sizes available to polyphagous mutillids is likely to vary from place to place, and site data on museum specimens are seldom precise enough to ensure that specimens are from the same populations. As an example of this site effect, we have found that *Dasymutilla pyrrhus* on the coastal dunes of Sanibel Island (Florida) average significantly smaller than the same species at the Archbold Biological Station, presumably because the only abundant potential host at Sanibel seemed to be a relatively small sphecid, *Microbembex monodonta* (Say). The range of host sizes is also likely to vary from year to year and even season to season, depending on fluctuation in populations of various hosts. Therefore, study of size variation in a population of velvet ants requires specimens collected within the same time period and from a small area, preferably one with a rich variety of hosts. This study controls these variables in a survey of mutillid populations in one location over one season.

METHODS

The Archbold Biological Station (ABS) is an ecological reserve of about 4,300 acres in Highlands County in south-central Florida. The ABS is on the Lake Wales Ridge, whose well-drained sand soils are ideal for fossorial hosts of velvet ants; the ABS has over 30 species of mutillids, some of which are very abundant. Collections were made in an area of sand pine (*Pinus clausa* Chapman) scrub and adjacent firelanes. The study site was a triangular area roughly $300 \times 200 \times 250$ m. The high mobility of mutillids observed within this area makes it unlikely that there are discrete subpopulations with different host populations within the study site. All specimens were collected in summer of 1984.

The hosts of many species of velvet ants are not known. Many hours of watching velvet ants at the ABS produced only a few observations of burrow-entering. The size allocations made by ovipositing velvet ants were therefore studied indirectly by capturing, drying, and weighing the adults that result from these allocations. Specimens were weighed rather than measured because the extreme sexual dimorphism in all species prevents comparison of linear dimensions. Males were collected in flight with an insect net and in Malaise traps. Females were collected in #10 tin can pitfall traps and from the surface of the ground. These methods may have biased our results if there is size-related mortality in one sex that is not matched in the other sex. Dried specimens were weighed on a Mettler H6 digital analytical balance (Mettler Instrument Co., Hightown, N.J.). We were not able to separate weights of soft and hard tissue; the former may vary with the age and nutritional state of the adult. We believe that in all specimens the age-related differences in dried soft tissues are insignificant compared with the weight of the non-varying soft tissues and the extraordinarily massive exoskeleton. The results were analyzed with the Mann-Whitney U-test (two-tailed) Siegel, 1956). Most of the specimens are in the collection of the Archbold Biological Station, with voucher series in the collection of Dr. Donald Manley (Florence, S.C.) and the Florida State Collection of Arthropods, (Gainesville, FL).

RESULTS AND DISCUSSION

The results are summarized in Table 1. The 13 species can be divided into 3 groups: those in which the females tend to be heavier (3 species), those in which the males tend to be heavier (7 species), and those in which there is no clear correlation between sex and weight (3 species).

SPECIES WITH LARGE FEMALES

The 3 species with large females follow the general rule among arthropods that where size dimorphism occurs the female is usually the larger sex, as can be seen in any collection of spiders or Orthoptera. The usual explanation for such dimorphism is that egg production and storage is directly related to size, whereas male reproductive success often depends more on agility and rapid development than on size (Darwin, 1881). Among provisioning and parasitoid Hymenoptera, which are able to allocate resources on the basis of sex, the limitation of resources results in a tendency to allocate more to females, for whom the reproductive penalty for small size is likely to be more severe. Additionally, it may be more efficient for a female to invest in a large number of small males rather than a few large males even when large males have higher reproductive success (Alcock et al. 1977).

TABLE 1. SIZE DIFFERENCES (DRY WT.) BETWEEN MALE AND FEMALE VELVET ANTS AT THE ARCHBOLD BIOLOGICAL STATION, FLO-
RIDA.

Species	n	Mean wt.	(mg)	Wt. range	(mg)	p ¹	Observed size
	♂	♂	♀	♂	♀		Difference
<i>Dasympatilla archboldi</i>	30	15.7	4.2	5.1-28.0	1.3- 9.5	<0.0001	Males Larger
<i>Ephuta f. floridana</i>	5	4.4	2.8	3.4- 8.9	1.6- 4.4	0.026	Males Larger
<i>Ephuta m. margueritae</i>	8	3.4	2.0	2.3- 5.5	1.4- 2.8	0.014	Males Larger
<i>Ephuta s. slossonae</i>	20	9.0	2.8	3.8-19.3	1.4- 4.4	<0.0001	Males Larger
<i>Photomoropus paulus</i>	114	4.7	3.2	2.2- 8.1	1.7- 5.3	<0.0001	Males Larger
<i>Timulla d. dubitata</i>	12	35.5	8.2	13.9-63.5	3.1-26.0	<0.0001	Males Larger
<i>Timulla floridensis</i>	47	17.2	5.6	3.8-36.2	2.2-11.1	<0.0001	Males Larger
<i>Dasympatilla asopus bevar</i>	6	21.5	24.9	16.0-28.1	14.3-29.6	0.3974	NS ²
<i>Dasympatilla castor</i>	71	10.5	8.4	3.5-12.4	3.4-11.5	0.3859	NS ²
<i>Dasympatilla nigripes</i>	17	7.9	9.2	4.0-13.2	4.9-16.0	0.24	NS ²
<i>Dasympatilla pyrrhus</i>	20	27.4	39.2	7.5-50.3	8.1-75.2	0.04	Females Larger
<i>Pseudomethoca oculata</i>	21	9.7	21.8	6.0-20.0	8.2-44.0	<0.0001	Females Larger
<i>Pseudomethoca sanbornii</i>							
<i>aetis</i>	12	11.5	15.0	8.4-18.3	5.8-25.1	0.025	Females Larger

¹Mann-Whitney two-tailed U-test.²No significant difference.

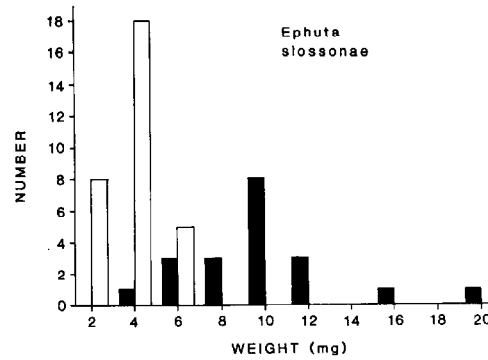
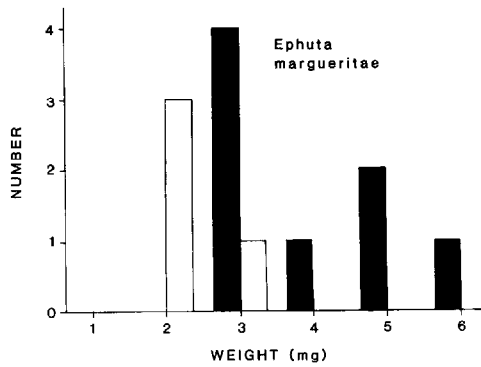
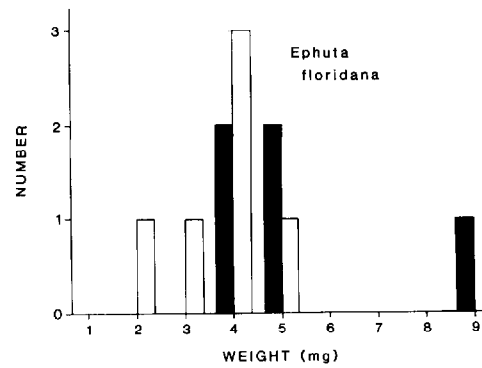
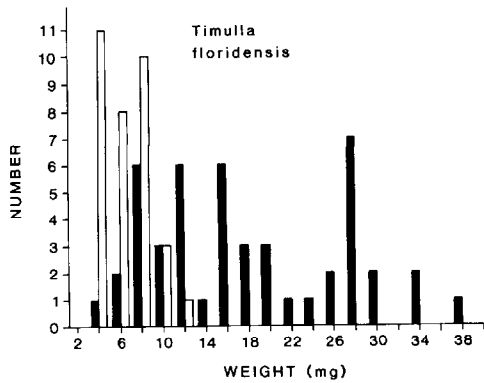
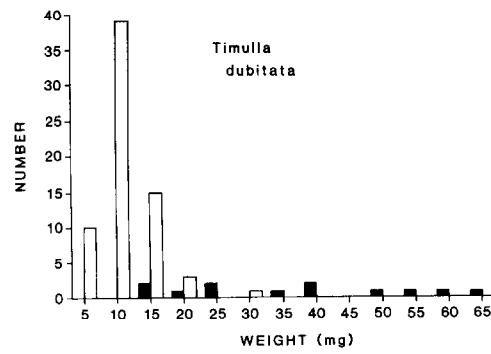
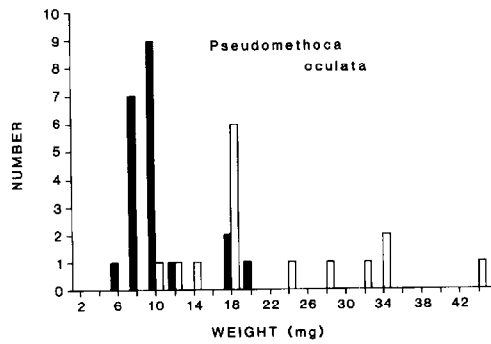
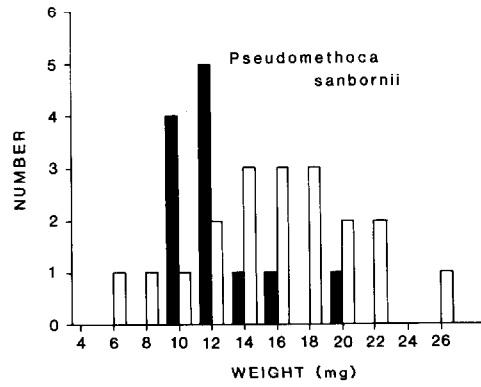
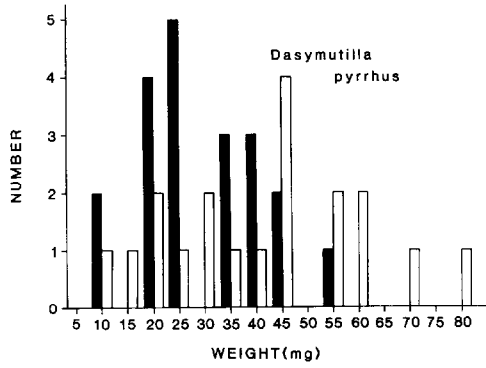
Dasymutilla pyrrius (Fig. 1) was the only species of 5 studied in the genus in which females are clearly heavier than males. The females also show great variation and a high standard deviation (18.2) in weight. At the ABS, we have often observed this species around nest aggregations of *Bembix sayi* Cresson and we have seen *D. pyrrius* entering the burrows of *B. sayi* and *B. texana* Cresson. A large number of *D. pyrrius* were found around the nesting aggregations of *Microbembex monodonta* on Sanibel Island. Since this species tends to attack aggregating burrowers, the ability to develop and store a number of eggs at a time may be an advantage of large females. On the other hand, there is clearly no absolute size criterion for allocation of hosts to a particular sex in this species, and this flexibility may be important in a species that attacks aggregating hosts, as a rigid adherence to host size as a determinant of sex could result in highly skewed sex ratios where there are aggregations of a uniform host.

In *Pseudomethoca sanbornii aetis* (Fox) (Fig. 2) and *P. oculata* (Banks) (Fig. 3) there may be an additional factor favoring large size in females. The head of the female of both species is greatly enlarged and might be used to block the host gallery if these species tend to spend a period of days in the host burrow, as in the case of *Pseudomethoca frigida* (Smith) (Brothers, 1972). The macrocephalic queens of eusocial halictid bees described by Wilson (1971) show a remarkable morphological convergence with female *Pseudomethoca* species. The known hosts of *Pseudomethoca* are halictids (Krombein, 1979), and it appears that the mutillids and the eusocial species of halictids may have independently evolved the same features that permit domination of a halictid burrow.

SPECIES WITH LARGE MALES

In the genera *Timulla* (Figs. 4, 5) and *Ephuta* (Figs. 6-8), the larger size of males is probably related to the male habit of carrying the female during courtship and copulation. Phoretic copulation has been reported in *Timulla oajaca* (Blake) (Linsley, 1960) and *T. dubitata* (Smith) (Sheldon, 1970). We have captured phoretic couples of *T. floridensis* (Blake), *Ephuta sabaliana* Schuster and *E. floridana* Schuster. Phoretic copulation with concomitant large males has been described in the families Bethyridae and Tiphidae as well as the Mutillidae (Evans, 1969). Large male size in certain Hymenoptera was noted by Darwin (1881, p. 279) who mentions the apterogynous tiphid *Methoca ichneumonides* Latreille. "The explanation of this anomaly is that a marriage flight is absolutely necessary with the species, and the male requires great strength and size in order to carry the female through the air." In species with wingless females (including all Mutillidae), phoretic copulation may have an important dispersal function, as the female may thus cross barriers such as streams (Evans, 1969). Phoretically copulating males may gain an advantage over potential rivals by obtaining sole possession of the female during flight. It has recently been shown (O'Neill and Evans, 1983) that phoretic behavior is a highly effective strategy for larger individuals among males of a species of sphecid; the female in this case is fully winged. Whatever the selective pressures that led to phoretic behavior in *Timulla* and *Ephuta*, the antiquity of phoresy in these genera is shown not only by the consistently large male size, but also by the modifications of the male clypeus and frons to accommodate the head of the female (Sheldon, 1970).

While phoretic behavior may select for size dimorphism, another factor may also select for small size in females of non-phoretic and phoretic species. If a species attacks burrowing hosts of differing sizes, large females may have difficulty entering the burrows of small host species. Where large size is not important for defense or for rapid egg storage and production, one would expect selection for small size in females of polyphagous velvet ants.



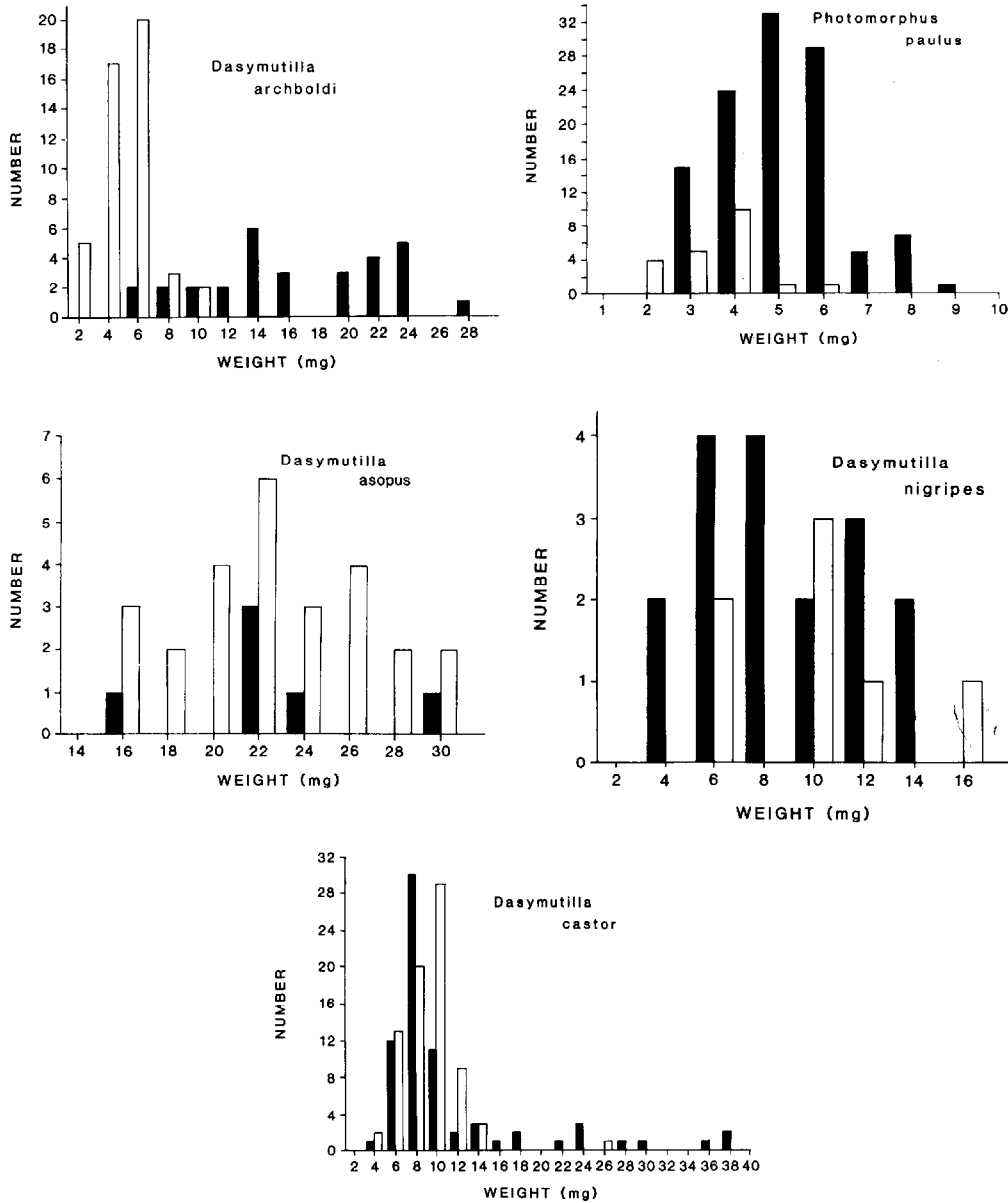


Fig. 1-13: Weights of Mutillidae spp. Solid bars are males, open bars are females.

This latter explanation for small female size may apply to *Dasymutilla archboldi* Schmidt and Mickel (Fig. 9), which shows a sexual size dimorphism as dramatic as those of *Ephuta* and *Timulla* species. There are no reports of phoretic copulation in *Dasymutilla* species, and male *Dasymutilla* show no modifications of the head or mandibles correlated with phoresy (Sheldon, 1970) or combat between males. Phoretic behavior in *D. archboldi* cannot be dismissed but seems highly unlikely. *Dasymutilla archboldi* appears to be a Florida endemic confined to a few former islands in the central part of the state, where the soil is very deep well-drained sand (Schmidt and Mickel, 1979). In the absence of some potential competitors, *D. archboldi* may have evolved an expanded host range to efficiently use both large and small hosts. No other eastern

Dasymutilla shows such striking and consistent size dimorphism. The most obvious relevant characteristic of the habitat of *D. archboldi* is the uniform sandy soil occurring over a large area; the consequence of this edaphic uniformity is that no burrowing bees or wasps, with the exception of *Bembix* and *Cerceris* species, appear to form aggregations. When hosts are diverse and very widely dispersed, small size in the female velvet ant is not limited by selection for rapid production and storage of many eggs, and adherence to host size as the determinant of sex is not likely to lead to gross imbalance in sex ratios.

Photomorphus paulus (Bradley) (Fig. 10) belongs to a genus whose biology is so poorly known that we hesitate to speculate on the significance of the relatively small size of the females. We suspect that phoresy does not occur in this species as we have captured hundreds of males in Malaise flight traps, and not one female. Out of a much smaller total number of *Ephuta* and *Timulla*, there were a number of females found in the traps, sometimes still in the grasp of the male.

There is a certain amount of overlap in the weights of males and females in all these species with large males. This overlap may be due to imprecise host measurement by ovipositing females, to negligible effects of size on fitness in either sex within the overlapping range, or to a tendency to balance sex ratios without ignoring any hosts.

SPECIES SHOWING NO SEX-BIASED SIZE VARIATION

Dasymutilla asopus bezar (Blake) (Fig. 11) and *D. nigripes* (Fabricius) (Fig. 12) show no significant sex-bias in size variation, though both species vary considerably in weight in both sexes. Females in these species may be indiscriminate in resource allocation, or there might be a pattern of resource allocation that is too subtle to be revealed in the small number of individuals in these samples. *Dasymutilla castor* (Blake) (Fig. 13) seems to show a pattern in host size utilization even though the statistical analysis shows no difference in sizes of males and females. The graph of frequency distribution shows in the range of 4 to 14 mg a pair of more or less normal distribution curves, with the females clearly heavier, much as in *D. pyrrius*. Above 14 mg, however, all but one of the 13 specimens were males. It is possible that in the lower size ranges the normal advantages of large female size prevail, but above a certain threshold the problem of gaining access to burrows may come into play as a selective pressure influencing the behavioral repertoire of the female.

CONCLUSION

The explanations of the data presented in this study are highly speculative and would not have been advanced if we had felt there was a practical method for eventually obtaining direct observations on the oviposition behavior and direct evidence of the effects of natural selection on various size classes of males and females. The principle value of the study is that it shows diversity of male-female size ratios in Mutillidae and focuses attention on the importance of resource allocation, which is only possible because of the male haploidy of higher Hymenoptera. Male haploidy might arise and be maintained as a mechanism to increase the maternal genome at the expense of the paternal genome (Bull, 1979); moreover male haploidy may be important in social Hymenoptera because it makes sisters more closely related to each other than to their offspring (Wilson, 1971). But the most direct benefit of male haploidy is that it permits optimal reproductive success by differential allocation of resources between the sexes in response to differences in the biological roles of the male and female.

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