

REPRODUCTIVE STRATEGIES OF DIURNAL MUTILLID WASPS (HYMENOPTERA: MUTILLIDAE)¹

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ABSTRACT. Seven species of diurnal mutillid wasps were collected in the Big Bend area of West Texas with the goal of determining reproductive strategies and other biological characteristics: (a) emergence strategies differed not only among species but, in some cases, from one emergence period to another within a given species, protogyny in six species may be a response to high risk of May air temperatures below the male activity threshold, and protandry in *Timulla suspensa* is attributed to uniquely late emergence and activity of females (mid-June to mid-July) and males' prior access to a reliable energy source in flowers of graythorn; (b) overwintering stage: four species overwintered as both immatures and adults; one species overwintered solely as adults; (c) maximum head size ranged from 76% to 156% greater than minimum head size, depending upon the species; (d) sex ratios varied from 0 to 1.33, depending upon the species; (e) allocation of male eggs based on adult host size: two species preferred large hosts, one preferred medium-sized hosts, three preferred small hosts; and (f) mode of reproduction: six species were arrhenotokous; one probably was thelytokous.

Phoresy in *T. suspensa* is believed to result in reduced competition for hosts after males and females congregate for copulation on graythorn. Both the female and the brachypterous male of *Myrmilloides grandiceps* possess cephalic spines that presumably anchor the head securely in the walls of the host burrow, an adaptation for inter- and intrasex combat.

INTRODUCTION

The study of reproductive strategies, including mating systems, offers excellent opportunities for insight into the mechanisms of natural selection and sexual selection (Charnov, 1982; Kawecki and Stearns, 1993; Godfray, 1994). Because reproduction is closely linked to Darwinian fitness, the consequences of different strategies can be determined more easily than with many other aspects of life history. Here, we are concerned principally with the mating systems of mutillid wasps (Hymenoptera: Mutillidae), commonly known as “velvet ants.” These insects are particularly interesting because ecological constraints appear to have led to some unusual mating systems, and these in turn can have profound consequences for other aspects of reproduction, especially the allocation of resources between female and male offspring (sex allocation) (Boulton et al., 2014). In most mutillid species the female deposits eggs on the larvae or prepupae of ground-nesting solitary bees and wasps. With few exceptions the adults are strongly sexually dimorphic, the females being wingless (apterous) and the males winged (alate). The limited data available on the host ranges of mutillid species in the United States suggests that many species are not highly specific. For example, *Dasymutilla asopus* (Cresson) has been recorded from two families of bees, *Pseudomethoca frigida* (Smith) from three genera of halictid bees, and *Sphaerophthalma amphion* (Fox) from four families of bees and wasps (Krombein, 1979). A key feature of mutillid biology—regular abrasion of the mandibles—was studied by Hennessey (2002). Although the abrasion rate changes regularly with time, it is nearly constant for all members of any given cohort at any given time. Members of different cohorts may be active at the same time, but collected individuals can be referred to a particular cohort based on mandible length as a fraction of head width. Mutillid mating systems differ in the method of sex determination, amount of sexual

dimorphism, and timing of male vs. female emergence (in protandry males emerge first; in protogyny females emerge first.) Given that most diurnal species of U.S. velvet ants are known from both sexes (Krombein, 1979), it can be assumed that most reproduce sexually by arrhenotoky, as do the large majority of hymenopterans (Flanders, 1956; Godfray and Cook, 1997). However, *Dasymutilla texanella* Mickel is known only from the female sex, and no males were found among the 23 individuals collected in the present study. This suggests that this species is thelytokous.

This diversity in mating systems has consequences for the evolution of sex allocation. The consequences are particularly interesting because, despite considerable theorizing, they have been the object of few empirical studies. In many arrhenotokous species, unmated (virgin) females may contribute a large proportion of the total number of eggs deposited. Eggs from unmated females are haploid and therefore male. An abundance of male eggs in turn selects for any mated females to produce a compensating excess of female offspring (Godfray, 1988, 1990). However, some mutillid females rely upon host size in choosing the sex of an egg, a behavior that would limit the ability to produce a compensating excess of females. Mutillids produce two or more generations per year (Hennessey, 2002), and differing male/female survival rates can lead to differences in opportunities for mating. For example, if males from a focal generation can mate with females from both their own generation and a previous generation, an excess of males may be favored in the focal generation (Werren and Charnov, 1978; Seger, 1983). The aim here is to document the mating systems of seven mutillid species and quantify several factors that could influence the evolution and consequences of these systems.

MATERIALS AND METHODS

STUDY AREA

Collections were made at two sites within the city limits of Alpine, Brewster County, Texas. Alpine (elev. 1,380 m) is located in the Davis Mountains, a range in the Chihuahuan Desert of West Texas. Annual rainfall in and near the city averages about 39 cm (Powell, 1998). The principal study site was a dirt road about 0.5 km long and 2 to 4 m wide, depressed as much as 2 m below the surrounding terrain. On 7 and 9 July

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Table 1 Sex ratio by size class.

Species, no. collected	Head width (mm)	Sex ratio ¹	n
<i>D. foxi</i> , 16♂♂, 55♀♀ (40♂♂, 56♀♀) ²	1.66 to 2.10	.37 (.44) ²	37 (39)
	2.11 to 2.58	.14 (.87)	26 (43)
	2.60 to 3.12	.55 (1.33)	9 (14)
<i>D. heliophila</i> , 6♂♂, 31♀♀	1.40 to 2.48	.21	35
	3.55 to 3.58	0	2
	1.42 to 2.18	.42	17
<i>D. snoworum</i> , 6♂♂, 30♀♀	2.24 to 2.70	.06	17
	3.55 to 3.59	0	2
	1.45 to 2.45	0	21
<i>D. texanella</i> , 0♂♂, 23♀♀	2.65 to 2.70	0	2
	1.78 to 2.48	0	16
	2.60 to 2.88	.20	18
<i>M. grandiceps</i> , 4♂♂, 34♀♀	2.95 to 3.14	.33	4
	1.20 to 1.75	.33	4
	1.76 to 2.08	.90	38
<i>P. propinqua</i> , 19♂♂, 52♀♀	2.12 to 3.43	0	29
	2.20 to 2.50	.37	37
	2.60 to 3.30	— ³	9

¹No. of males divided by no. of females.²Parenthetical numbers include all individuals collected on sunflower.³No females collected.

1990, male mutillids were also collected on flowering sunflower (*Helianthus annuus* L.) growing about 70 m from the west end of the road. The vegetation type near the principal study site was desert scrub, the dominant species being *Senegalia greggii* (Gray), *Mimosa aculeaticarpa* Ortega, and *Prosopis glandulosa* Torrey. Along the road itself were dense stands of a small, blue-flowered annual, *Machaeranthera tanacetifolia* (H. B. K.) Nees, and three 1.5-m-tall plants of graythorn, *Ziziphus obtusifolia* (T. and G.) Gray. Both species were highly attractive to solitary bees, the principal hosts of many mutillids.

COLLECTION OF SPECIMENS

The road was searched one or twice each afternoon for about 45 min between 1600 and 1800 hr on 9 June through 28 Aug 1990. A total of about 115 hr were spent collecting on these and other dates (indicated below). Males were collected with an insect net and killing jar. Females generally were collected by gently pinching them between thick layers of cloth and releasing them into a killing jar. Several flowering, 1-m-tall plants of graythorn also were examined daily because they were highly attractive to males of various species of mutillids, as well as to females of *Timulla* spp. An effort was made to collect every mutillid seen; however, several females of *Timulla suspensa* (Gerstaecker) escaped capture on graythorn. By 11 July 1990 ground vegetation had become so dense that relatively few mutillids were seen either in the air (males) or on the ground. Daily afternoon searches were conducted again on 6 Aug 1993 and from 30 Aug to 15 Sep 1997. About 30 additional specimens were collected on several occasions in Aug 1989, Aug 1993, May 2001, June 2004, and May 2007.

Of the 34 species of diurnal mutillids identified at the study site, the seven most abundant were selected for study (Table 1). A total of 94 males and 253 females of these seven species were collected.

Intensive collection of female mutillids from such a small area (ca. 2,000 m²) would reduce population levels if the number of hosts parasitized were proportional to the number of female mutillids searching for hosts. However, the correlation may be high only when host populations greatly outnumber mutillid populations, and in any case, the current study provides no means for estimating the correlation between these two variables. Hypothetically, intensive collecting might shift the sex ratio in favor of males, but again, in the present study any such a shift would be undetectable.

Various bee species were abundant at the principal study site, while ground-nesting wasps were much less common.

Voucher specimens were deposited in the insect collection of the Natural History Museum of Los Angeles County. Daily maximum temperatures in Alpine were recorded with a maximum/minimum thermometer.

MEASUREMENTS AND EXAMINATIONS OF BODY PARTS

Head widths of all collected females and males were measured (see Hennessey, 2002) with an ocular micrometer in a stereo microscope at 40× magnification. Mandible lengths of females were measured to the nearest 0.01 mm (mandibles of males and mandibles of female *Myrmilloides grandiceps* (Blake) were not measured because none were abraded and thus could not be used to estimate age). Mandibular abrasion is a well-known phenomenon in insects, including the bee *Halictus tripartitus* Cockerell (Packer et al., 2007). Scanning electron micrographs of the head of a male *M. grandiceps* were made at 40× magnification.

Adult mutillid head width was used as a proxy for overall host size. The use of a proxy provides insight into the range of hosts attacked by each mutillid species, because mutillid head width can be assumed to correlate well with host size (the actual hosts remain unidentified). However, it must be stipulated that in some mutillid species, notably *M. grandiceps*, the head is unusually large compared with the meso- and metasoma. Therefore, interspecies comparisons of host size must be made with caution, particularly in the case of *M. grandiceps*. Generally, only a single adult mutillid emerges from each parasitized host, although exceptions are known (Brothers, 1984).

RESULTS

SEX RATIOS

The species-specific sex ratios (number of males divided by number of females) were as follows: *Dasymutilla foxi* (Cockerell) .30 at principal study site, .68 at principal and secondary study sites combined. *Dasymutilla heliophila* (Cockerell) .20; *Dasymutilla snoworum* (Cockerell and Fox), .20; *D. texanella*, 0; *M. grandiceps*, .12; *Pseudomethoca propinqua* (Cresson), .37; *T. suspensa*, .70. Sex ratios in each species were different in different-sized hosts (Table 1): *D. foxi*, *M. grandiceps*, and *T. suspensa* preferred to deposit male eggs in large hosts; *P. propinqua* preferred medium-sized hosts; and *D. heliophila* and *D. snoworum* preferred small hosts. No males of *D. texanella* were collected.

EMERGENCE AND ACTIVITY PERIODS

Emergence and activity periods of six species are represented in Figures 1A to 1F. Newly emerged females were identified by their relatively long, unabraded mandibles. Clusters of data points representing these females are enclosed in boxes. Aging females were identified by their abraded mandibles, and their age was inferred to be proportional to the amount of abrasion. Aging females belonging to the same cohort and, in a few instances, overwintered females that could not be distinguished from them on the basis of mandible wear are enclosed by parallel lines extending below and to the right of each box. Numbers of males collected are indicated at the appropriate date at top of each graph. In five species, females with shortened mandibles were collected before or during the first emergence of new adults. These females, presumably overwintered adults, appear in the graphs as unenclosed data points.

D. foxi

New adult females (Fig. 1A) emerged early in the season (9 to 24 May) in 1990 at the same time that overwintered adult females resumed

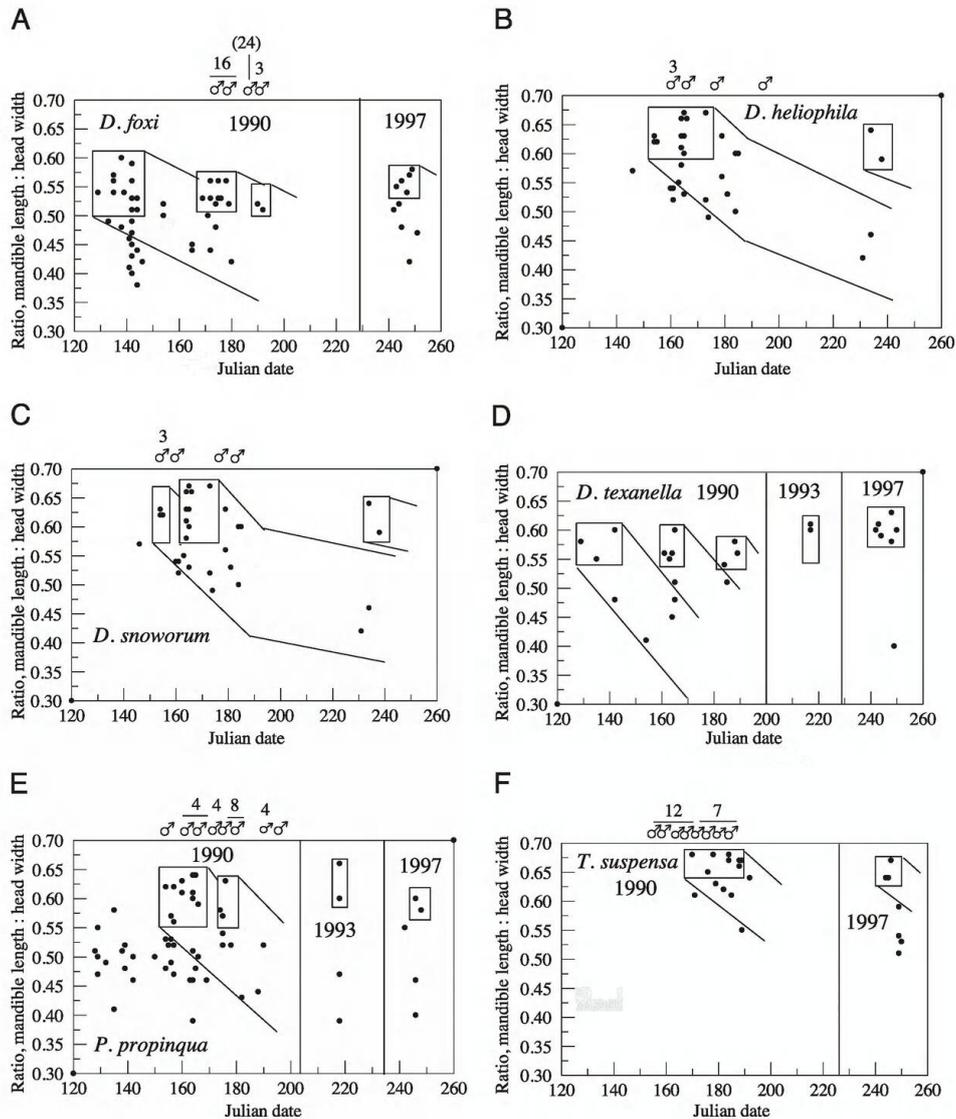


Figure 1 Emergence and activity periods: A, *D. foxi*; B, *D. heliophila*; C, *D. snoworum*; D, *D. texanella*; E, *P. propinqua*; F, *T. suspensa*. Boxes, newly emerged females; bands, older females; unenclosed data points, females presumed to have overwintered as adults. Numbers of males collected indicated above top border of graph.

activity. During this period, overwintered females constituted 46% to 58% of the population. The first males were collected on 23 June during the second period of female emergence. Males at the principal study site tended to concentrate on flowers of graythorn, whereas males at the secondary study site concentrated on sunflower.

D. heliophila

The first female of 1990, apparently one that had overwintered, was collected on 26 May (Fig. 1B). The first of the new generation in 1990 emerged during three periods beginning on 2 June. A female of an apparent second generation emerged on 21 Aug 1997.

D. snoworum

The first female of 1990, apparently one that had overwintered, was collected on 26 May (Fig. 1C). Females and males of the first new generation in 1990 emerged during two periods beginning on 3 June.

D. texanella

The first newly emerged female of 1990 was collected on 10 May (Fig. 1D). No males were collected, nor have males ever been reported in the literature.

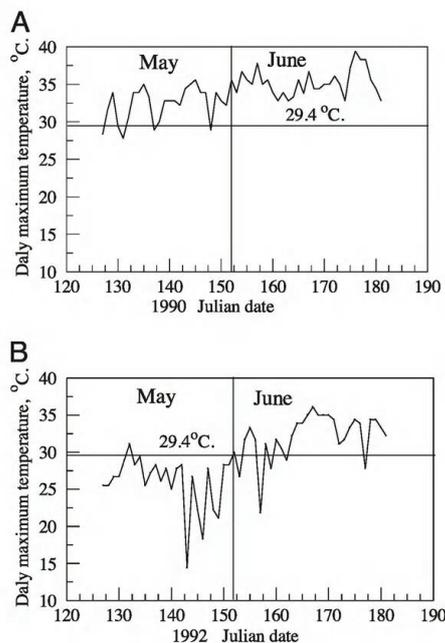


Figure 2 May and June air temperatures in Alpine, Texas. A, 1990; B, 1992.

P. propinqua

In 1990 the first females, apparently all overwintered, were collected on 9 May (Fig. 1E). Overwintered females remained active through the entire first emergence period of new females (3 to 15 June). During this time they constituted 56% of the total population of *P. propinqua* females. Males tended to concentrate on flowers of graythorn.

T. suspensa

In 1990 the first males emerged on 2 June, and 63% of males were collected between then and the first emergence of females 15 days later (Fig. 1F). With the single exception of a male collected *in copulo* on a stem, males were collected only from flowers of graythorn. Females were collected only on stems and leaves of the same plants.

M. grandiceps

Females (not shown in graphs) were first collected on 9 May 1990, and the last was collected on 7 Sep 1997. Males were collected in 1990 on 22 May, 2 June, and 9 June. It was not possible to determine accurately the emergence patterns because the mandibles of both males and females were unabraded.

ACTIVITY THRESHOLDS

Daily maximum temperatures in May and June of 1990 and 1992 are shown in Figures 2A and 2B. Activity thresholds were determined as the lowest maximum daily temperature at which specimens were collected on any day in any year of the study. Thresholds for females of *D. snoworum*, *D. texanella*, *P. propinqua*, and *T. suspensa*, and for males of the latter two species, ranged from 29.1°C to 30.5°C. Because 1.4°C was such a small range, the mode, 29.4°C, was taken as an approximation for the purpose of establishing a horizontal activity threshold line in

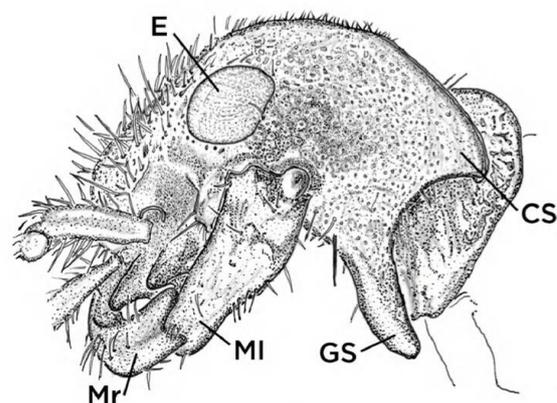


Figure 3 Head of male *M. grandiceps*, left anterolateral view (maxillary and labial appendages not shown). Abbreviations: E, left compound eye; CS, left carinal spine; MI, left mandible; Mr, right mandible; GS, left subgenal spine.

Figure 2. Activity thresholds for *D. foxi* and *M. grandiceps* were somewhat higher at 33.4°C and 32.2°C, respectively.

STRUCTURE OF MYRMILLOIDES GRANDICEPS

The head of a female *M. grandiceps* constituted 35% of the total body weight (6.7 mg) compared with 16% for the head of a female *D. foxi* (total body weight, 17.0 mg). The head was similarly large in male specimens of *M. grandiceps* (Fig. 3). Other conspicuous characters were: (1) compound eyes small in both males and females; (2) antennal scapes with bases protected dorsally by a pair of large, carinate antennal tubercles; (3) mentum with margin bearing a pair of large, anteriorly directed spines; (4) mandibles .75 to .80 times the head width compared with .55 to .68 times the head width in other species studied; (5) secondary mandibular tooth as large as the primary tooth and situated at the distal tip of the mandible rather than at midlength, as in the other species studied; (6) subgenal spines about .30 and .20 times the total head thickness in males and females, respectively, and (7) cephalic carinae developed as a pair of large, posteriorly directed spines.

DISCUSSION AND CONCLUSIONS

EMERGENCE AND ACTIVITY PERIODS

It is suggested that one important factor underlying the diversity of mutillid mating systems is a large difference between the longevity of the sexes and consequent differences in exposure to daily maximum temperatures below the activity threshold. Air temperatures in May 1992 were well below those during the same period in 1990 (Fig. 2). The long-lived females might survive for extended periods at unseasonably low temperatures, just as they survive low winter temperatures and resume activity when temperatures warm. However, males might not live long enough to resume activity at warmer temperatures.

The latest recovered female of *D. foxi* from the first emergence period in 1990 was collected on Julian day 180, 56 days after the apparent end of the first emergence period (Fig. 1A). The latest recovered female of *D. snoworum* from the first emergence period was collected on Julian day 234, 60 days after the apparent end of the first emergence period (Fig. 1C). A more extreme example of longevity was found in *P. propinqua* (Fig. 1E). Assuming that overwintered *P. propinqua* females became dominant at the end of Sep 1989, the oldest female of that species was

collected 273 days, that is, more than 9 months, after the beginning of dormancy. Females of other species with severely worn mandibles may have been even older. The mandibles of a large *D. foxi* female collected on 21 May 2001 were severely worn with tips separated by a gap of 0.07 mm. This female, with an age index of .37, probably belonged to the first emergence cohort of the preceding year, in which case she would have been a full year old when collected. Females of some other species are similarly long-lived. Females of *Dasymutilla vesta* (Cresson) may live more than 10 months, and females of *Dasymutilla nigripes* (Fab.) may live as long as a year (Hennessey, 2002). Females of *Dasymutilla occidentalis* (L.) may also live up to a year (Schmidt, 1978). Because mandibles in males are not abraded, male longevity must be estimated by other, less certain, methods. Males of the eastern species *D. vesta* and *D. nigripes* survived as long as 22 days and 12 days, respectively, after the end of the preceding emergence period (Hennessey, 2002). Deyrup and Manley (1990) reported that many males of *Pseudomethoca oculata* (Banks) and *Pseudomethoca simillima* (Smith) “must live a month or less.”

Overwintered adult females, but not males, were found in all six species that displayed abraded mandibles (i.e., all but *M. grandiceps*). Hennessey (2002) reported overwintering of adult females of *D. nigripes*, *D. vesta*, and *Timulla vagans* (Fab.). Schuster (1951) collected fertilized females of *Ephuta* sp. in January, indicating overwintering in those species. Evans and Miller (1969) noted the overwintering of marked individuals of *D. nigripes*, and Potts and Smith (1944) observed hibernation of *Dasymutilla aureola* (Cresson). Hence, overwintering of adult females appears to be common among diurnal mutillids.

No males of any species were collected from 9 May to 2 June (Fig. 1) despite the collection of a total of 41 females of *D. foxi*, *D. heliophila*, *D. snoworum*, and *P. propinqua* during that period. Deyrup and Manley (1990) reported that female *P. oculata* (Banks) and *P. simillima* in Florida “are active in spring and summer, when there are no records of males.” Jellison (1982) observed dozens of female *P. propinqua* on sunflowers in Montana, and only “a few weeks later 4,000 to 10,000 females and males in a nearby vacant lot.” Manley and Taber (1978) remarked that in April 1977 a population of *D. foxi* north of Tucson, Arizona, was limited to females and that “no males were observed until mid-May.” Schmidt and Hook (1979) observed high densities of female *P. simillima* in late March 1978, but “no males [were] collected.” According to O’Neill (2001), “protandry is a common feature of the life histories of male solitary wasps,” but clearly mutillids do not fit this pattern.

According to Degen et al. (2015), “protogyny is not rare in insects,” and in working with a Lepidoptera model, they argue that longer life expectancy of females compared with males favors the evolution of protogyny. However, perhaps the most important reason for protogyny in female diurnal mutillids is simply that the apterous females search for hosts on the ground, whereas alate males search for females in the air. By late afternoon, the peak period of mutillid activity, ground temperatures are generally higher than air temperatures.

Each species appears to deal with risks of early-season subthreshold temperatures in a somewhat different way. *Dasymutilla foxi* females emerged early in the 1990 season just as females that had overwintered as adults resumed activity. The first males of this species did not emerge until the middle of the second period of female emergence. Likewise, *P. propinqua* females appeared early in 1990, but abraded mandibles indicate that all had passed the winter as adults, and there was no early emergence of either sex; rather, both females and males delayed emergence until 3 June. With the exception of one overwintered female collected on 26 May, *D. snoworum* emergence and activity was delayed until 3 June. Probably, overwintered *D. snoworum* females also were active during the

emergence period, even though, apart from one exceptional female, none were collected until 9 June. Females of *D. texanella*, like those of *D. foxi*, emerged early, probably at the same time that overwintered females resumed activity. Females of *T. suspensa* did not emerge until very late, 18 June, but unlike the case in other species, males had already begun to emerge 13 days previously, a pattern known as protandry.

The large proportion of *T. suspensa* males collected on graythorn flowers may have been maintaining their energy stores in waiting for females to emerge.

ALLOCATION OF MALE EGGS BASED ON HOST SIZE

Pitts et al. (2010) discussed the allocation of male eggs based on host size in the mutillid *Sphaerophthalma pensylvanica* Lepeletier. Charnov et al. (1981) explained the tendency of parasitoid wasps to produce smaller males by pointing out that large size usually benefits females more than males. While this explanation may apply in some degree to the Mutillidae, large size probably prevents female mutillids from entering the nests of small hosts (Deyrup and Manley, 1986). A small female can easily crawl through either a large or small burrow, but a large female would have to increase the diameter of the burrow along its entire length to reach its host. Such digging would entail high energy costs and would no doubt rapidly abrade the mandibles. Although the possibility of such digging cannot be entirely excluded, the uniformity of mandible abrasion rates within a given cohort implies that large females do not, in fact, enlarge burrows. Uniform instantaneous abrasion rates are manifested as distinct cohort boundaries that remain parallel over long periods of time, that is, weeks to months (Fig. 1) (Hennessey, 2002). How many hosts a female finds must vary considerably by chance, and large females finding many small host burrows would have more opportunities to dig than large females finding few such burrows. Mandibles of “lucky” females would be expected to abrade faster than those of “unlucky” females, thereby making cohort boundaries spread with time and making the data points resemble a scatter diagram. Since the boundaries remain parallel, it appears that large females do not dig their way to small hosts. Mandibular abrasion is more likely the consequence of digging into and out of the soil in a regular diel pattern.

In female mutillids, different combinations of body size, type of sex determination (whether arrhenotoky or thelytoky), mating status (in arrhenotokous species), and size of potential hosts present varied opportunities for reproduction. As previously mentioned, narrow burrows protect small hosts from parasitization by large females but admit small females. Wide burrows admit both mated and unmated females of all sizes. A small, mated female can deposit eggs of either sex in either large or small hosts, but the sex of the eggs depends upon the pattern of host use displayed by the particular species. For example, females of *T. suspensa*, whether mated or not, deposit only male eggs in large hosts because males must be large enough to carry phoretic females of the next generation. In contrast, small females of *P. propinqua*, whether mated or not, deposit male eggs only in small hosts. Both large and small mated *P. propinqua* females deposit female eggs principally in large hosts. It is believed that the pattern displayed by *P. propinqua* is common in insects because an increase in size benefits females more than males (Fisher, 1930).

LARGE SIZE OF *DASYMUTILLA FOXI* MALES

The large size of *D. foxi* males may be explained by the advantages of enhanced flying capability. Twenty-four of the total of 40 *D. foxi* males were collected on sunflower plants growing about 70 m from one end of the main study area. Some of these 24 males may have emerged outside the main study area in a landscape rendered relatively unfavorable for mutillids by dense ground vegetation. However, most probably originated within the study area and flew to the sunflower plants,

attracted by extrafloral nectaries (Rogers, 1985). Therefore, it may be that *D. foxi* females preferentially deposit male eggs in large hosts (Table 1) because large males are able to fly longer distances than small males in search of food.

FEMALE-BIASED SEX RATIOS

It is apparent in Table 1 that the species in the present study follow the general rule of female bias in parasitoid wasps (see Quicke, 1997). However, the reason for this bias in the six arrhenotokous species in this study is not clear and might depend on a multiplicity of factors, such as those described by Werren and Charnov (1978), Charnov (1982), Seger (1983), and West et al. (2002).

The most extreme case of female bias occurs in *D. texanella*, which appears to be thelytokous. No mutillid species has ever been recognized as thelytokous; however, the male of *D. texanella* has never been reported in the scientific literature, nor were any males of this species found in the present study despite the collection of 23 females. Thelytoky would give *D. texanella* the ability to persist at low population levels when males might have difficulty in finding mates and would avoid the problem of frequent male inactivity due to subthreshold air temperatures, especially early in the season. *Dasytilla texanella* may have solved the problem of frequent early-season subthreshold temperatures by doing away with males altogether.

Although rare, examples of thelytokous Hymenoptera are known. Examples are the parasitic wasps *Venturia canescens* Gravenhorst (Ichneumonidae) and *Leptopilina clavipes* (Hartig) (Figitidae) (Leach et al., 2009) and the bees *Apis mellifera capensis* Escholtz (Oldroyd et al., 2008), *Ceratina dallatorreana* Friese (Daly, 1966), and *Nomada japonica* Smith (Maeta et al., 1987).

PHORESY IN *TIMULLA SUSPENS*A

Females of most species tend to be larger than males (Deyrup and Manley, 1986), but males in the phoretic species of the diurnal genus *Timulla* are larger than the females that they transport (Linsley, 1960; Deyrup and Manley, 1986). Alate males of *T. suspensa* averaged 93% larger than the apterous females that they are presumed to transport. A copulating pair of a very similar species, *Timulla oajaca* (Blake), were captured in flight at the site of the present study (see also Linsley, 1960). The large male of *Nemka viduata* (Pallas) (Mutillidae) transports the smaller female (Tormos et al., 2010). Alate females of the bethylid *Apenesia nitida* (Kieffer) and the tiphiid *Dimorphothynnus haemorrhoidalis* (Guerin) are larger than the apterous males that they transport (Evans, 1969). Alate males of *Timulla dubitata* (Smith) and *Timulla floridensis* (Blake) are much larger than the phoretic females (Sheldon, 1970; Deyrup and Manley, 1986). O'Neill and Evans (1983) and Osten (1999) hypothesized that phoresy allows male Hymenoptera to avoid interference by rival males. Evans (1969) noted that "the female [of *Timulla*] may cross barriers such as streams," and Lin (1964) and Evans (1969) saw phoresy as a means for escaping from predators. However, present observations of *T. suspensa* suggest a different explanation—that phoresy in this species allows females to avoid intrasex competition for hosts.

In 1990 the first *T. suspensa* males of the season were collected on flowers of graythorn. Fifteen days later, females, many presumably unmated, began gathering on branches of the same plants. The limited period of host availability and the restricted hours of female mutillid activity would exert strong selective pressure on females to begin host searching immediately after copulation. In studies by Evans et al. (1973) and Hennessey (2002), *D. nigripes* females were widely distributed and therefore did not have to compete intensely for hosts immediately after copulation. The generally low dispersal rates (44% of recovered females <1m/day, 75% <2m/day) found by Evans et al. (1973) would not be

disadvantageous in that situation. However, in the present study, *T. suspensa* females that had congregated for mating on graythorn plants would be exposed to intense competition if they descended to the ground and immediately began searching. The initial host searches would be especially concentrated since the graythorn plants were located at the edge of a gravelly area unsuitable for mutillid activity. There, dispersal distances of 1 and 2 m would correspond to search areas of only 0.4 and 1.6 m², respectively. Any *T. suspensa* females that could disperse rapidly out of an area of intense competition would have a great advantage, as would the males whose genes the females were carrying. In *T. suspensa*, phoresy is the means of gaining this advantage.

In *T. suspensa*, phoresy allows males and females to improve their mate-searching efficiency without paying the penalty of intrasex competition. Enhanced mate-searching efficiency might allow a population to maintain itself at lower densities than would otherwise be the case. In a desert environment where rainfall is highly variable and host populations diminish during hot summers, an ability to find mates at low densities might sometimes save a population from local extinction.

It should be remarked that the reproductive advantage of phoresy to males must compensate for increased metabolic costs. The metabolic rate of a flying locust increases 0.79 times as fast as lift (Weis-Fogh, 1964). If the same relationship is true of *T. suspensa*, a male transporting a female would consume about 40% more energy than a male flying unencumbered.

Seasonal activity patterns may shed further light on the importance of phoresy in *T. suspensa*. At the elevation of Alpine, spring wildflowers bloom most profusely in late March through early May. Numerous adult solitary bees become active then to exploit the abundant source of pollen. By the second half of May 1990, the progeny of this first annual generation of bees matured as late larvae and prepupae. Females of *D. foxi*, *D. snoworum*, *M. grandiceps*, and *P. propinqua* then became active to exploit the newly available supply of hosts. (As mentioned previously, males of species with strong sexual dimorphism were inactive early in the season because of the high risk of subthreshold activity temperatures.) However, females of *T. suspensa* did not appear until June 18, which would coincide with the maturation of the next generation of bee larvae. Although it is possible that *T. suspensa* utilizes species of hosts that do not appear in suitable developmental stages until mid-June, it seems more likely that the long delay in the appearance of females results from the obligatory nature of phoresy in this species. Until air temperatures rise in mid-June, *T. suspensa* males are at risk of being unable to fly, and until the males fly, the females cannot be transported to new sites.

INTER- AND INTRASEX COMBAT IN *MYRMILLOIDES GRANDICEPS*

Males of many mutillid species fly in sinusoidal paths near the ground where they can readily detect sex pheromones emitted by the ground-dwelling females. However, the search areas of the brachypterous males of *M. grandiceps* would be smaller by orders of magnitude. Females would be too small to produce large quantities of sex pheromones, and the small quantities that could be produced would be diluted and scattered by air turbulence in the wake of low-lying vegetation such as *M. tanacetifolia*, which was abundant along the road where mutillids were collected. Furthermore, relatively low population densities (i.e., low compared with, say, many agricultural pests) would make the alternative of random searching inefficient. Taken together, these facts suggest the existence of specialized mate-searching behavior in *M. grandiceps*.

Much about the mating system of *M. grandiceps* can be inferred from morphology. Some of the male's cephalic armaments (Fig. 3) resemble

those of the flightless males of the Australian sweat bee, *Lasioglossum erythrum* Cockerell (Kukuk and Schwartz, 1998). These male bees fight each other inside the host burrow for access to communally nesting females. Wheeler (1927) coined the term “phragmosis” to describe an arthropod’s use of a specially modified body structure to block the entrance to its nest. Phragmosis is especially well documented in certain ants (Fischer et al., 2015), and the term would seem to apply also to *M. grandiceps* with its radically modified, flattened head.

Like the male sweat bees, males of *M. grandiceps* have reduced wings, enlarged heads, and powerful mandibles, although the wings of *M. grandiceps* are even more reduced and the head and mandibles even larger. A male might take up residence in a host burrow either to defend its offspring against intrusion by other males or to defend unparasitized hosts within the burrow while awaiting arrival of an unmated female. The head of *M. grandiceps* has two modifications of particular interest: two pairs of large spines projecting posteriorly and a pair of extremely large subgenal spines projecting ventrally (Fig. 3). When the head is in the prognathous position, the subgenal spines would be embedded like stakes in the walls of the burrow, allowing the head to serve as a stable platform for brandishing the anteriorly directed, scythe-like mandibles.

In the hypognathous position, the cephalic teeth would serve as the stabilizing stakes. There are many similar examples in insects of projections that anchor body parts inside a burrow or case. The abdomen of predaceous larvae of cicindellid beetles bears a pair of anteriorly directed dorsal hooks (Peterson, 1960) that grab the walls of the burrow to prevent the larvae from being dragged out by prey. The ultimate abdominal segment of larvae of the trichopteran *Macronemum* sp. terminates in a pair of hooks that apparently anchor the larva inside its case in the swift-moving rivers that it inhabits (Peterson, 1960). The chrysidid wasp *Praestochrysis shanghaiensis* (Smith), an inquiline parasitoid like *M. grandiceps*, uses its terminal abdominal spines to brace itself as it chews through the sticky wall of the cell protecting its host (Yamada, 1991).

It would be expected that defending males of *M. grandiceps* would occasionally be confronted by mated females as well as other males. Mated females would seek to enter the host burrow to parasitize the immature bees, but these are the same hosts that the defending male’s mate would need to parasitize in order to pass along the male’s genes. Therefore, the male would be expected to defend the nest against entry by any intruding, previously mated female. Very likely, larger males of *M. grandiceps* are more effective in inter- and intrasex combat than smaller males (although it is unclear why the same argument would not apply to females).

The female’s cephalic armaments are nearly identical to those of the male except for somewhat smaller posteriorly directed teeth in the female. Once again, formidable armaments imply defense of a host burrow. Females of *P. frigida* were frequently observed in combat with their host bees, *Lasioglossum zephyrum* (Smith) (Lin, 1964). After ovipositing, females of *Dasyutilla scaevola* (Blake) remain in the host burrow and fight with conspecific females over ownership of the burrow (Alan Hook as quoted in Quicke, 1997). The cephalic armaments of *M. grandiceps* females indicate that they too defend their young in this manner. Furthermore, since a male’s entry into the burrow might attract another female, a defending female probably also kills or drives away intruding males.

The mating system of *M. grandiceps* constrains opportunities for adopting new hosts. The head-stabilizing spines of an individual, whether male or female, that guarded the burrow of a larger-than-usual host would not function effectively in the larger burrow. Consequently, outsized individuals would be selected against. Adoption of a new, smaller than usual host would be impeded by the usual difficulty of entering a burrow narrower than the mutillid’s head capsule.

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