

POPULATION-LEVEL CHARACTERISTICS OF *DASYMUTILLA NIGRIPES*,  
*D. VESTA*, AND *TIMULLA VAGANS* (HYMENOPTERA: MUTILLIDAE)

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## ABSTRACT

A total of 308 females and 182 males of *Dasymutilla nigripes* (Fab.), *D. vesta* (Cresson), and *Timulla vagans* (Fab.) (Hymenoptera: Mutillidae) were collected during 1996 and 1997 in a cleared vacant lot in a deciduous forest in Maryland. Mandibles of females abraded at rates that varied with time of year but were very similar for all members of any given cohort at any specific time. The number of generations varied from 1 to 3 per year depending on the species and year. Some adult females of each species overwintered, and during one 15-day period in 1996 overwintered females of *D. vesta* were estimated to constitute more than 60% of the total female population. Exceptional females were estimated to live as long as 10 to 12 months although 2 to 2½ months was more typical. In early and mid-season, males generally emerged synchronously with females, but relatively few males were collected during late-season emergences of females. In some cases, discrete size ranges of adults indicated that as many as 4 different sizes (and therefore presumably different species) of hosts were attacked in different years or at different times within the same year.

Key Words: emergence, overwintering, longevity, voltinism

## RESUMEN

Cuatrocientos noventa machos y hembras de *Dasymutilla nigripes* (Fab.), *D. vesta* (Cresson), y *Timulla vagans* (Fab.) fueron coleccionados a lo largo de la orilla de un bosque deciduo en Maryland durante 1996 y 1997. La edad de las hembras se calcularon midiendo la cantidad de desgaste mandibular. Los machos emergieron, por lo general, simultáneamente con las hembras. Las hembras adultas invernantes consistieron del 0 al 62.5% del total de la población femenina adulta. El número de generaciones mostró una variación de una a tres, dependiendo de la especie y el año. Las hembras adultas de mayor edad vivieron hasta un máximo de 10 a 12 meses. Según indicado por el ancho de la cabeza de las hembras adultas, *D. vesta* y *T. vagans*, atacaron huéspedes de distintos tamaños (y en consecuencia, probablemente distintas especies de huéspedes) durante diferentes tiempos y en distintos años.

Most North American species of Mutillidae, or "velvet ants," are parasitoids principally on mature stages of ground-nesting Hymenoptera (Krombein 1979). Most species are arrhenotokous, females developing from fertilized eggs and males from unfertilized eggs. Although arrhenotokous species cannot maintain themselves indefinitely without producing males, stable local populations of *D. dugesii* (Cockerell & Casad) may consist entirely of females for a month or more during early spring when air temperatures would be too low for males to fly (Hennessey, unpublished). Males of another arrhenotokous species, *Myrmilloides grandiceps* (Blake), have vestigial wings and are active on a warm soil surface even during periods of low air temperatures (Hennessey, unpublished). *D. texanella* Mickel may gain some advantages of both sexual and asexual reproduction through automictic thelytoky (Hennessey, unpublished). These and other mutillid species offer rich opportunity for the study of mating systems and reproductive biology. However, despite the intrinsic

interest of the Mutillidae, relatively little is known about their biology. In the United States, only three life history studies have been published, two by Brothers (1972, 1978) and one by Ferguson (1962). Brothers (1978) cites only a few other studies published in Europe.

Females of *Mymosula parvula* (Fox) and *Pseudomethoca frigida* (Smith) crawl down the tunnel of the host bee into a cell containing the host pupa or prepupa and deposit an egg which eventually develops into an adult that digs its way to the soil surface (Brothers 1972, 1978). Brothers (1978) summarized unpublished observations by Cotrell (1936) indicating that *Dasymutilla bioculata* (Cresson) has a similar life history.

Knowledge of population-level phenomena in mutillids is even more scant than knowledge of life histories. Manley and Spangler (1983) described differences in flight activity periods of male *Dasymutilla* in Florida, but there appear to be no detailed studies of population-level phenomena in the world literature on Mutillidae. The

dearth of detailed studies might result from the difficulty of making frequent collections over a long period and, heretofore, the lack of a means for estimating the age of adults.

To help fill the gap, this paper reports results of a 2-year study of certain population and life cycle characteristics of *Dasymutilla nigripes* (Fab.), *D. vesta* (Cresson), and *Timulla vagans* (Fab.). The major characteristics studied were timing of emergences of males and females, amount of above-ground activity between emergences, abundance of overwintered females, female longevity, and seasonal and year-to-year changes in the choice of hosts. It is hoped that these descriptions of general patterns in three mutillid populations will provide a useful background for future interpretations of different patterns shown by certain other mutillid species. It is also possible that the technique used to determine the age of adult female mutillids might be applicable to other mandibulate insects.

In the present study, amount of mandible wear was used as an estimator of female age. This method was used by Houston (1981) and Butterfield (1986) in studies of carabid beetles and by Zouhourian-Saghiri et al. (1983) in studies of *Locusta migratoria*. Daly (1963) distinguished old from young halictid bees, *Hemihalictus lustrans* (Cockerell), by the amount of mandible wear and attributed the wear to the bees' burrowing behavior. Also, Wallin (1988) demonstrated that mandibles of the carabid *Pterostichus melanarius* Illiger abrade with age and attributed the abrasion to the beetle's fossorial habit.

Seasonal and annual changes in host-size preferences were inferred from measurements of head width. U.S. species of mutillids are, as far as is known, solitary parasitoids that entirely consume their hosts. Adult mutillids therefore closely resemble their hosts in size. Mickel (1924) attributed bimodal size variation in female *D. bioculata* to the parasitization of 2 different-sized host species. Sex-based size variation is well-known in the Mutillidae (Deyrup & Manley, 1986). Of course, host species can be positively identified only by excavating subterranean nests, an effort not within the scope of the study.

#### MATERIALS AND METHODS

In Aug. 1995 a 2-ha area of mature deciduous forest in Bowie, Prince George's County, Maryland was bulldozed down to the bare soil surface. Native forest remained on the north and south sides of the study area. Male and female mutillids were collected in the lot 5 or 6 times per week in 1996 from 15 July to 15 Oct. and in 1997 from 8 June to 23 Aug. and from 10 Sept. to 30 Sept. During the period 24 Aug. to 9 Sept. 1997, collections were made on a total of only 3 days. During both years of the study, the forest was searched occa-

sionally for mutillids up to a distance of 2 m from the southern edge of the lot. All individuals of *D. nigripes*, *D. vesta*, and *T. vagans* that were found were collected. Representatives of 11 other species were also collected occasionally. To ensure that the study would cover the entire annual period of activity each year, the lot was searched for at least 1 week before the 1st specimen was collected and for at least 1 week after the last specimen was collected.

To determine the age of individuals, mandibles of males and females of all species were examined for signs of wear, i.e., blunting and shortening. Mandibular length was measured in all females of *D. nigripes*, *D. vesta*, and *T. vagans*. These species were selected for measurement because many specimens had worn mandibles and long series of specimens were collected throughout the active seasons of both years. In the unextended position one mandible, either right or left, is folded over the other. The overlying mandible was measured from the base of the posterior mandibular condyle to the tip of the apical tooth (Fig. 1). Mandibles of males were not measured because none showed signs of wear.

Because mutillids typically show considerable intrapopulation variation in overall size, maximum head width of females of *D. nigripes*, *D. vesta*, and *T. vagans* was measured along with mandible length so that the latter quantity could be expressed as a fraction of the former. Mandible lengths of small and large females of the same species could thereby be directly compared.

Head width of both males and females was measured in dorsal view across the widest part of the head, i.e., at the posterior extent of the eyes in

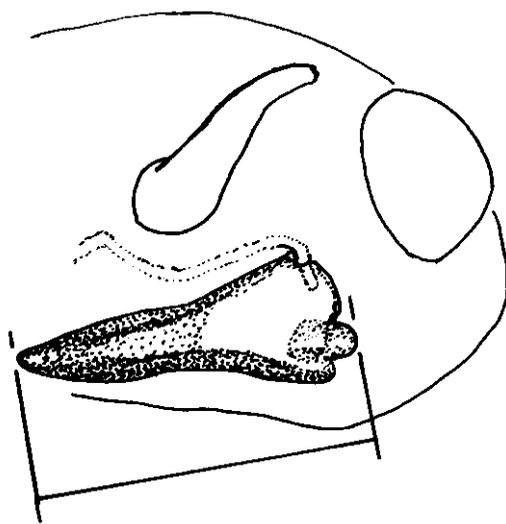


Fig. 1. Measurement of mandible length in females of *Dasymutilla vesta*, *D. nigripes*, and *T. vagans* (*D. vesta* figured).

the case of *D. nigripes* and *D. vesta* (Fig. 2A) and just anterior to the posterior extent of the eyes in *T. vagans* (Fig. 2B).

All species were determined by the author. The principal keys used were those of Mickel (1936, 1937) and Manley (1991).

## RESULTS

### Preferred Habitat

Thirteen species of mutillids were collected. Most females were collected within 3 m of the forest edge. The most productive areas in early and mid-season were patches of bare or sparsely vegetated soil contiguous with the forest. Bare patches that were separated from the forest by even a few cm of dense growth (e.g., grasses and small herbaceous plants) or dry twigs yielded relatively few specimens. Five small, scattered areas totaling about 500 m<sup>2</sup> produced nearly all of the female mutillids collected. Males were collected over a broader area except during Aug. 1996 when they concentrated on profuse flowers of *Chamaecrista fasciculata* (Michaux) Greene (Caesalpinaceae). As temperatures declined in late season, female mutillids became scarce on exposed soil and much more abundant in a 1 m-wide zone just inside the forest edge.

### Occurrence of Mandible Wear in Various Genera

Mandible wear was evident in at least 1 female of each of the following species (numbers indicate numbers of females examined): *Dasymutilla gibbosa* (Say) 4, *D. nigripes* 57, *D. scaevola* (Blake) 4, *D. vesta* 119, *Pseudomethoca simillima* (Smith) 6, *Timulla dubitata* Mickel 5, *T. vagans* 132. These species are relatively large, females averaging 7 to 10 mm in length.

Mandibles of all females examined of the following species showed no obvious signs of wear (numbers represent numbers of females examined): *Ephuta margueritae* Schuster 30, *Myrmosula parvula* (Fox) 3, *Photomorphus banksi*

(Bradley) 2, *P. johnsoni* Viereck 21, *Pseudomethoca frigida* 64, *Sphaerophthalma pennsylvanica* (Lepelletier) 2. All 12 females of *Myrmosula* sp. (Tiphidae) also had unworn mandibles. Except for *S. pennsylvanica*, the sole diurnal representative of an otherwise nocturnal genus, these species are relatively small, females averaging 4 to 5 mm in length.

No males of any species showed noticeable signs of wear.

### Emergence Clusters and Population Cohorts of Females

In general, beginnings of emergence periods were marked by the appearance of specimens with long (i.e., unworn) mandibles. The emergence period labeled "97-2" in Fig. 3A serves as a typical example of emergence in *D. nigripes*, *D. vesta*, and *T. vagans*. Eight females of *D. vesta* with long mandibles (.60 to .64) were collected from 4 to 11 July; these were considered to be members of the 97-2 emergence cluster. A specimen with long mandibles (.61) collected on 16 July was not assigned to this cluster because it was separated from the latest-collected member of the cluster by a hiatus of 5 days. Similarly, the specimen collected on 1 July was not placed in the 97-2 cluster because it was separated from the 1st-collected member of that cluster by a hiatus of 3 days and because it was referable to the preceding cohort, 97-1. Therefore, a box was drawn around the 8 data points of 4 to 11 July to indicate their cohesiveness as an emergence cluster.

In Figs. 3A, 4A, and 5A individual females of *D. vesta*, *D. nigripes*, and *T. vagans* were assigned to population cohorts based on degree of mandible wear. In *D. nigripes* and *D. vesta* all members of a given cohort lay within an arcuate band of constant width originating in an emergence cluster and continuing to the end of the season. Cohorts of these 2 species remained distinct throughout the year, i.e., no data points appeared in empty spaces separating adjacent bands, even late in the year when bands might be expected to broaden and overlap due to random differences in amounts of wear. In other words, although rates of mandible wear decreased after emergence, the rates of mandible wear at any given moment were approximately equal for all members of a cohort. Rates of mandible wear varied somewhat among all 3 species, but in all species wear rates began in the range of 3 to 6  $\mu\text{m}$  per day and declined regularly throughout the season, reaching lows of approximately 0.5  $\mu\text{m}$  per day or less around 1 Sept.

In 1997 females of *T. vagans* (Fig. 5A) emerged in 4 episodes, the 1st 2 separated by only 3 days and the 2nd 2 separated by only 5 days. Because the variability in mandible length of newly emerged females was high (.62 to .68) and emergences were closely spaced, each cohort soon overlapped with succeeding cohorts.

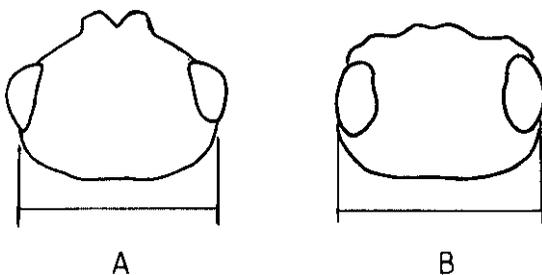


Fig. 2. Measurement of maximum head width in *Dasymutilla vesta* and *D. nigripes* (A), and *Timulla vagans* (B).

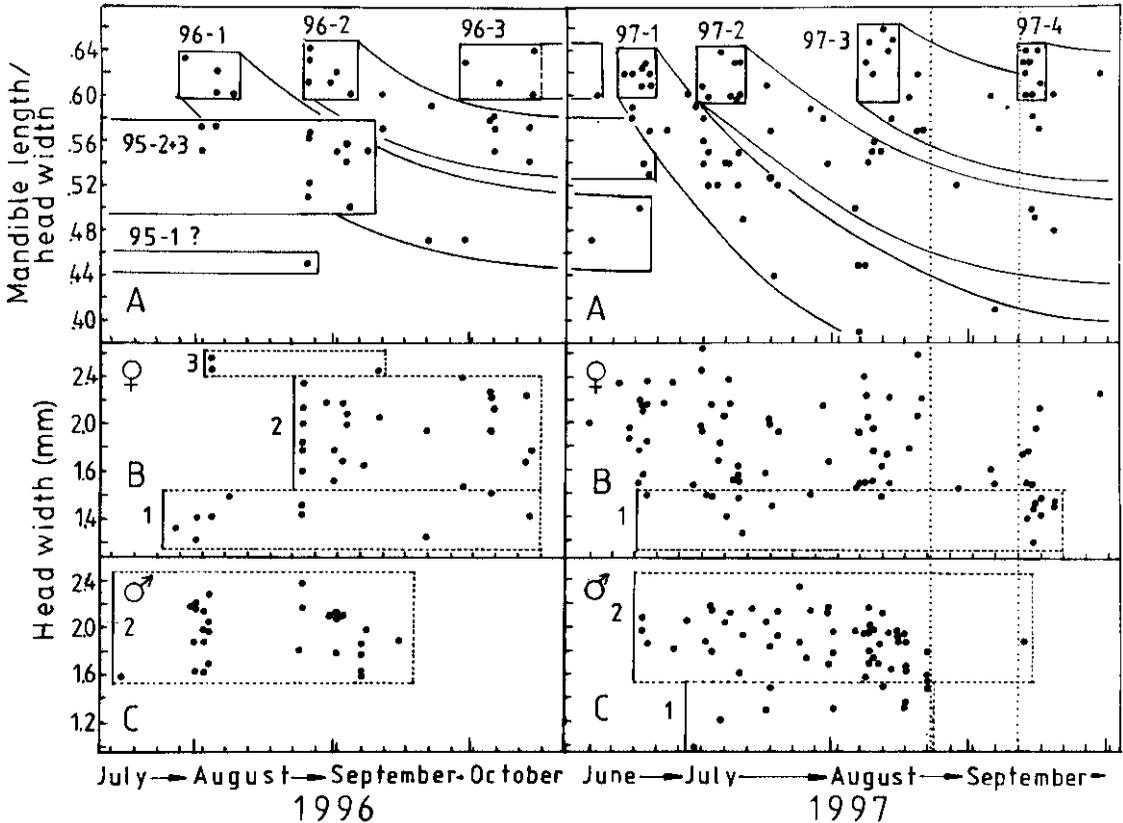


Fig. 3. *Dasyutilla vesta* collected in 1996 (left graphs) and 1997 (right graphs). Vertical dotted lines in 1997 mark the period (24 Aug.-9 Sept.) when collections were made on only 3 dates. A. Cohorts of adult females as determined by relative mandible length. Boxes along top of figure enclose emergence clusters; arcuate bands enclose older females belonging to the same cohort. Elongate rectangles at left (1996) enclose females believed to have overwintered as adults. B. Head widths of adult females (an indicator of overall body size and size of host). Numbers identify discrete size ranges of hosts. C. Head widths of adult males. Numbers identify discrete size ranges of hosts.

Some data points in Figs. 3A, 4A, and 5A did not, upon 1st examination, appear to be associated with any emergence cluster. For example, in 1997 the first 2 specimens of *D. nigripes* (Fig. 4A) were collected 12 and 13 days prior to the first emergence cluster, 97-1, that began on 4 July. Moreover, mandibles of these 2 individuals and 1 additional specimen collected on July 4 were extremely short (.41-.55) compared to those of cluster 97-1 (.69-.78). These and similar data points in Figs. 3A and 5A are represented as continuations of cohorts that emerged during the previous year; i.e., the apparently anomalous points are considered to represent females that overwintered as adults.

The activity of overwintered females of *D. vesta* was synchronized with emergence periods in 1996 (early Aug., and late Aug. through early Sept.) and 1997 (mid-June). The activity of overwintered females of *T. vagans* was synchronized with emergence periods in 1996 (late July through early Aug.).

Although *D. vesta* females showed the same size range in 1996 and 1997 (Fig. 3A), in 1996 the heads of early-emerging females (late July to early Aug.) were either large (about 2.4 mm) or small (1.1 to 1.5 mm). Mid-sized females (1.6 to 2.3 mm) did not begin to emerge until late August.

## DISCUSSION

### Emergence Periods and Generation Times of Females

**Definition of "emergence"** The term "emergence" as it is used here refers to the emergence of adult mutillids from the subterranean nests of their hosts onto the soil surface. It is not known whether adults delay in digging to the soil surface after emerging from the pupal cuticle, although Brothers (1972, 1978) did not mention such a delay in *M. parvula* and *P. frigida*.

*D. nigripes*. Two emergence periods of *D. nigripes* females designated 96-2 and 96-3 were evident in 1996 (Fig. 4A). The 3rd began only 15

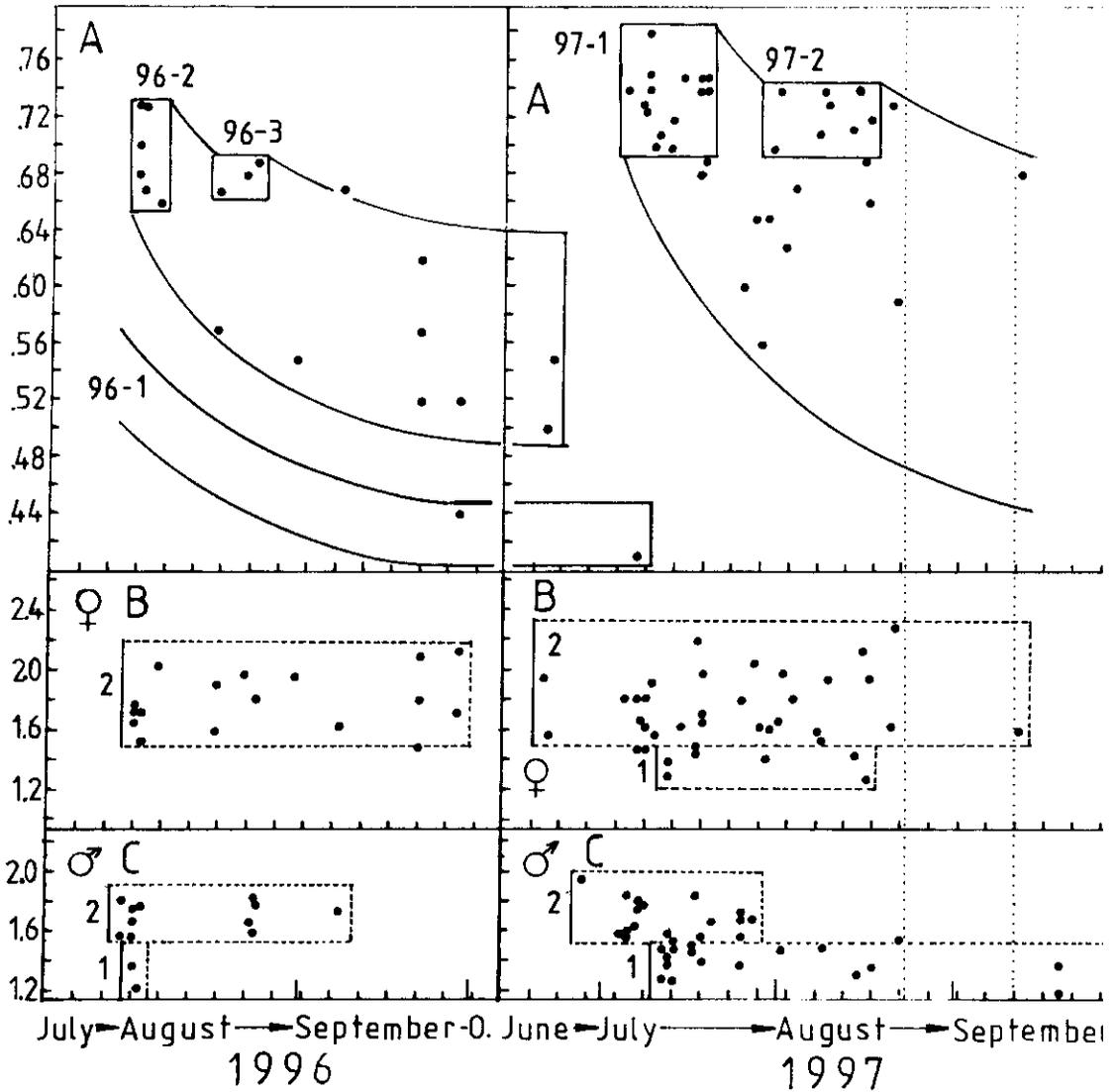


Fig. 4. *Dasymutilla nigripes* collected in 1996 (left graphs) and 1997 (right graphs). Vertical dotted lines in 1997 mark the period (24 Aug.-9 Sept.) when collections were made on only 3 dates. A. Cohorts of adult females as determined by relative mandible length. Boxes along top of figure enclose emergence clusters; arcuate bands enclose older females belonging to the same cohorts, some of which overlap. Narrow arcuate band crossing bottom of figures for 1996 and 1997 encloses females believed to have overwintered as adults. B. Head widths of adult females (an indicator of overall body size and size of host). Numbers identify discrete size ranges of hosts. C. Head widths of adult males. Numbers identify discrete size ranges of hosts.

days after the 2nd began, probably too short a time for them to be different generations. However, a single female with severely worn mandibles (.44) was collected near the end of Sept. clearly belonged to an earlier cohort, 96-1. Hence, it appears that a small 1st generation in late June or July produced a larger generation that emerged during 2 periods. The start of the 2 emergence periods in 1997, 97-1 and 97-2, were separated by 26 days, suggesting that in that year *D. nigripes* also produced 2 generations. It is pos-

sible that the 97-1 and 97-2 emergences were synchronized to the life cycles of different host species, in which case the 97-1 females would not necessarily be the parents of the 97-2 females. Emergence data on *D. vesta* and *T. vagans* might be similarly interpreted.

*D. vesta*. In 1996 *D. vesta* emerged during 3 periods separated by at least 30 days (Fig. 3A). These periods probably represent discrete generations. In 1997 *D. vesta* emerged during 4 periods. The 2nd (97-2) began 18 days after the 1st. Because 18

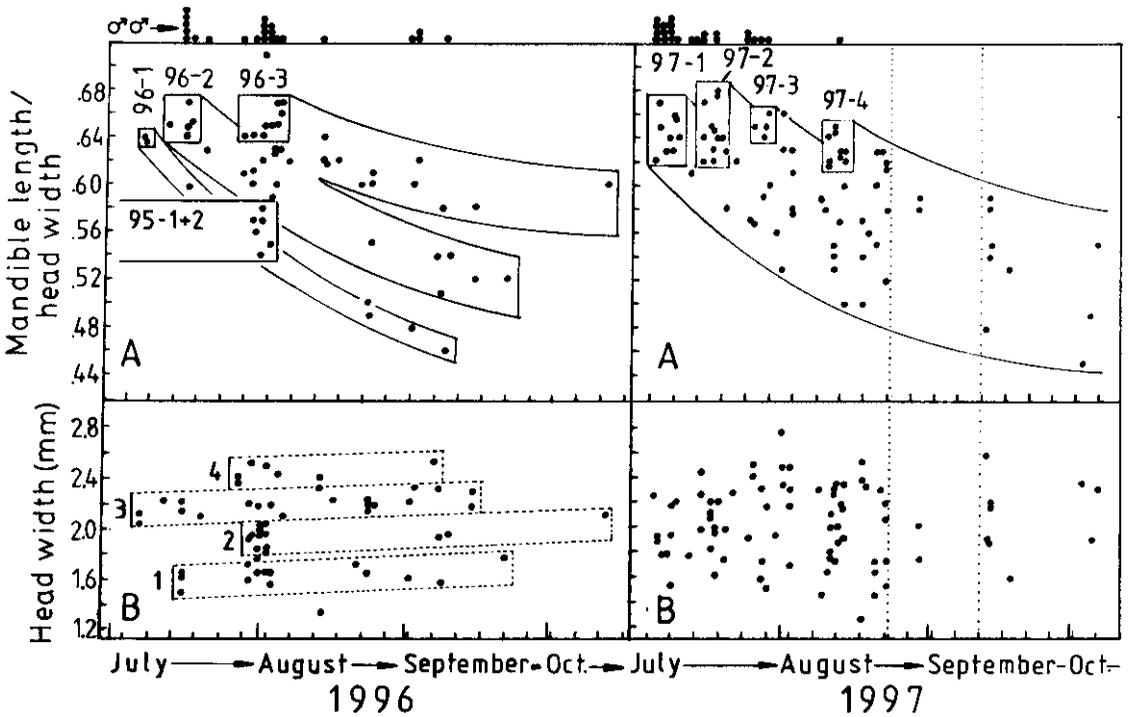


Fig. 5. *Timulla vagans* collected in 1996 (left graphs) and 1997 (right graphs). Vertical dotted lines in 1997 mark the period (24 Aug.-9 Sept.) when collections were made on only 3 dates. A. Cohorts of adult females as determined by relative mandible length. Boxes along top of figure enclose emergence clusters; arcuate bands enclose older females belonging to the same cohort (cohorts overlap in 1997). Elongate rectangle at left (1996) encloses females believed to have overwintered as adults. Dots above the figure indicate number of males collected. B. Head widths of adult females (an indicator of overall body size and size of host). Numbers identify discrete size ranges of hosts.

days is a full week less than the life cycle times of *M. parvula* and *P. frigida* reported by Brothers (1972, 1978), emergence clusters 97-1 and 97-2 may not represent discrete generations. Emergence periods 97-3 and 97-4 were separated from each other and from 97-2 by at least 38 days, a strong indication that these were 2 discrete generations.

*T. vagans*. Emergence periods 96-1 and 96-2 are close enough (5 days separation) to be emergences of the same generation. Period 96-3 began 21 days after the beginning of 96-1 (Fig. 5A), 4 days (16%) less than the 25-day life cycle of *M. parvula* and *P. frigida* (Brothers 1972, 1978). To determine whether or not 96-3 represents a later generation than 96-1 and 96-2 combined, it is helpful to consider the date of first male emergence, 14 July. Before that date females did not have the opportunity to mate and so could not have produced female progeny. The 1st female in period 96-3 emerged on 27 July, only 13 days after the 1st males appeared. Because 13 days was almost certainly insufficient time to complete development, the 1st female in 96-3 probably was not the offspring of any female in period 96-2. The remaining females in period 96-3 emerged from 30 July to 4 Aug., 16 to 21 days after the 1st males of

the year appeared. Therefore, it is very possible that some females in period 96-3 were of the same generation as those in 96-1 and 96-2. In 1997 (Fig. 5A) the 1st 2 emergence periods of *T. vagans* began only 10 days apart; consequently they represent staggered emergences within the same generation. The remaining 2 emergences, 97-3 and 97-4, were separated by only 17 days and so probably also represent a staggered emergence.

Female Longevity and Mixed Generations

The discovery of a method for recognizing overwintered females also enabled estimates of female life span. Two females of *D. vesta* collected in mid- to late June 1997 appear to have emerged in late July to early Aug. 1996 indicating a life span of more than 10 months (Fig. 3A). One female of *D. nigripes* (Fig. 4A) with severely worn mandibles (.41) collected in early July 1997 (see band 96-1) could not be definitely associated with any emergence cluster in 1996, but when the band is extended back in time (to the left) it originates in early July when the earliest females of *T. vagans* were collected. Therefore, *D. nigripes* female .41 may have been as old as 12 months at the time of collection.

Some females of all 3 species were active through the emergence periods of subsequent generations. For example, 1 1st-generation female of *D. vesta* that had emerged in late July or early Aug. 1996 (Fig. 3, 96-1) and 6 2nd-generation females that had emerged in late Aug. or early Sept. (96-2) were collected during the 3rd emergence period (96-3) in late Sept. and early Oct. Furthermore, during period 96-3, 1st- and 2nd-generation females outnumbered 3rd-generation females by 7:4. Assuming that adult mutillids emerged just as parasitizable stages of hosts became available, it can be inferred that the 1st emergence period in mid-June of 1997 (97-1) included offspring of 3 different generations (96-1, 96-2, 96-3). Similarly, the 3rd emergence cluster in 1996 (96-3) may have consisted principally of 1st-generation offspring of overwintered females (95-2+3). In fact, it seems likely that, despite the usual discreteness of emergence periods, all generations of all 3 species were mixed to some extent.

#### Interemergence Activity

Emergences of female mutillids almost certainly coincide with the development of parasitizable life stages (late larvae and prepupae) of the principle host species. Nevertheless, many females were collected during long periods between emergences. Six males and 4 females of *D. vesta* were collected between the 2nd and 3rd emergence periods in 1996 (Fig. 3A). Two males and 3 females were collected between the 1st and 2nd emergence periods in 1997, and 19 males and 11 females were collected between the 2nd and 3rd emergence periods of 1997. Quite possibly this inter-emergence activity is a search for secondary hosts whose life cycles are not synchronized with those of the primary hosts.

#### Rates and Causes of Mandible Abrasion

The inverted arcs drawn around population cohorts of females (Figs. 3A, 4A, and 5A) indicate decreasing rates of mandibular abrasion. The shape of the mandibles themselves may account for some of the decrease since the sharp tips (Fig. 1) would wear away faster than the thicker, basal portions. However, if the tapered shape of the mandibles were the only reason for decreasing rates of wear, all cohort bands would have the same slope at any given time after emergence. For example, the slope of a band 20 days after an emergence beginning in mid-June would be the same as the slope of a band 20 days after an emergence beginning in early Aug. Clearly this was not the case in *D. vesta* and *T. vagans* (Figs. 3A and 5A); in these species, bands at any specified time after emergence sloped less at the end of a year than at the beginning. Hence, an additional, unknown factor(s) must have caused mandible wear.

No doubt *D. nigripes*, *D. vesta*, and *T. vagans* abrade their mandibles to some extent as they tunnel through the soil in search of their ground-nesting, hymenopterous hosts. Nevertheless, the coherence of the cohort bands, especially late in the season of activity, cast doubt on the importance of tunneling in search of hosts as an important cause of mandibular abrasion. Fig. 5A provides the clearest example of band coherence. Two newly emerged females of *T. vagans* were collected on 6 July 1996, and 5 additional specimens were collected between 16 July and 9 Sept. Over the apparent 45-day life of the cohort, mandibles abraded at an average rate of 8.0  $\mu\text{m}$  per day. An average wear rate of only 0.5  $\mu\text{m}$  per day greater than, or less than, the average of 8.0  $\mu\text{m}$  would have placed a female outside the narrow arcuate band by Sept. 9. Hence, mandible abrasion rates of females differed by no more than 6% over the life of this cohort.

Tunneling in the soil for hosts does not appear to be a satisfactory explanation for this relatively uniform abrasion rate because finding the right place to tunnel must involve a large element of chance. If mandibles were substantially abraded in connection with host-searching activities, lucky females (i.e., those finding many host nests) would abrade their mandibles faster than unlucky females, and cohort bands would consequently widen with time until they merged and became indistinguishable. Similar instantaneous rates of mandible abrasion throughout a cohort imply a digging behavior which all female members of the cohort share to an equal extent. For example, mutillid females might share a diurnal rhythm such as tunneling out of the soil at the beginning of a favorable host-search period and back into the soil at the end of the period. If this explanation is correct, other, unknown factors must modify the depth of the digging and thus the rate of mandible abrasion because (1) the slopes of the bands for *D. vesta* were generally shallower in 1996 than in 1997 (Fig. 3A), (2) in all 3 species band slopes were always greatest during the weeks following emergence regardless of the season of emergence; i.e., the band slope of any given cohort decreased through both the increasing temperatures of summer and the declining temperatures of fall (Figs. 3A, 4A, and 5A), and (3) as the year progressed, each succeeding cohort had an overall band slope that was shallower than the band slope of the preceding cohort (Figs. 3A and 5A).

It may be significant that mandible wear was observed in 8 of the 9 large (average 7-10 mm) mutillid species but not in any of the 5 small (average 4-5 mm) mutillid species nor in the small tiphiid, *Myrmosa* sp. Possibly, mandibles of small species are not abraded because the insects do not dig into the soil. Surface debris and cracks may offer alternate hiding places.

### Overwintering of Females

*D. vesta*. The mandibles of 9 *D. vesta* females positioned directly below cluster 96-2 in Fig. 3A were worn to lengths (.50-.57) that would place them in the 96-1 cohort band. However, these 9 were medium-sized (size range #2, Fig. 3B), whereas the preceding emergence cluster, 96-1, consisted only of large (size range 1) and small (size range 3) individuals. The small sample sizes do not permit a definite conclusion, but the most likely explanation for the incongruous size of the 9 females is that they belonged to prior cohorts. Since no cohorts of mid-sized females emerged earlier in 1996, the 9 females are referred in Fig. 3A to cohorts that originated in 1995. This interpretation is supported by the anomalous female with mandible so severely worn (.45) that she definitely could not have belonged to cohort 96-1. According to this interpretation, 62.5% (10/16) of the total population of *D. vesta* females in late Aug. and early Sept. 1996 had overwintered as adults.

*T. vagans*. A similar situation was seen in *T. vagans* (Fig. 5A). Six individuals with worn mandibles (.54-.58) were collected between 29 July and 2 Aug. 1996. However, their head widths did not correspond to the head widths of the females in the only preceding emergence cluster. The 6 individuals in question were in size ranges 2 and 4 (Fig. 5B), whereas the preceding females were in size ranges 1 and 3. Accordingly, these 6 individuals are figured as overwintered representatives of a cohort that emerged in 1995, and they comprised 24% of the total female population in late July and early Aug.

The scientific literature contains few reports of overwintering or overwintered female mutillids. Evans & Miller (1969) recovered 3 females of *D. nigripes* in Michigan in July, 1969 that had been marked during the summer of 1968. Potts & Smith (1944) collected 1 overwintering female of *D. aureola pacifica* (Cresson) in California.

### Host Utilization

Although identification of host species was outside the scope of this study, changes in utilization of unidentified hosts were apparent in Figs. 3B, 3C, 4B, 4C, 5B, and 5C. These figures present data on host sizes. In interpreting the figures it must be recalled that the sizes of adults in any given generation reflected the sizes of the hosts parasitized by females of the previous generation.

According to the interpretation already presented under the heading "Overwintering of Females," it appears that in 1995 *D. vesta* parasitized large, medium, and small hosts. The same female size ranges recurred in 1997, indicating the utilization of the same sizes of hosts in 1996 as in 1995. A comparison of the data for males in 1996 and 1997 (Fig. 4) reveals a different

situation. The 1st small male (1.3 mm) was collected 10 days after the end of the 1st female emergence, and small males continued to be collected until late Aug. during the 3rd female emergence. Therefore, males developed in small hosts during both 1996 and 1997. However, no small males were collected in 1996, indicating that few or no small hosts had been parasitized in 1995.

### Emergence and Activity Periods of Males

Generally, males of *D. nigripes*, *D. vesta*, and *T. vagans* were most abundant during and just after emergences of females. The only example of sustained male activity during an interval between female emergences was seen in *D. vesta* in 1997 (Figs. 3A and 3C). Another clear pattern was the decrease in male abundance at the end of the season of female activity. For example, no males of *D. vesta* were collected during the final female emergence period in 1996, and only 1 was collected during the final female emergence period in 1997. Declining air temperatures are the most likely explanation.

### SUMMARY AND CONCLUSIONS

Population-level characteristics were investigated by determining the age of individual females. This was accomplished by collecting specimens throughout the active seasons of 2 years and comparing the ratio of mandible length to maximum head width among different females of each species. Mandibles abraded at rates that varied regularly, permitting accurate estimates (plus or minus several days) of emergence dates. When mandible: head ratios were graphed as a function of Julian date, the shapes of the graphs suggested indirectly that females abraded their mandibles by digging through the soil in a diurnal rhythm other than host-searching.

The mutillid species studied had 1 to 3 discrete generations per year. Emergences of adults probably were synchronized with the development of parasitizable stages of the primary hosts. Although discreet, most or all of the generations probably were mixed, with adults of as many as 3 different generations emerging during one period. Typically, emergences continued for 5 to 10 days, although some were longer and others were interrupted briefly. In several instances overwintered females became active during the 1st and/or 2nd emergence periods. In some cases overwintered females were abundant in the general female population, reaching 64.5% of the total female population during the 2nd emergence of *D. vesta* in 1996. Females lived as long as a year, although a shorter life span was more typical. Males generally emerged synchronously with females but had shorter life spans. Males became scarce or absent altogether as fall approached and air temperatures declined.

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## REFERENCES CITED

- BROTHERS, D. J. 1972. Biology and immature stages of *Pseudomethoca f. frigida*, with notes on other species (Hymenoptera: Mutillidae). Univ. Kansas Science Bull. 50(1): 1-38.
- BROTHERS, D. J. 1978. Biology and immature stages of *Myrmosula parvula* (Hymenoptera: Mutillidae). Jour. Kansas Entomol. Soc. 51(4): 698-710.
- BUTTERFIELD, J. E. L. 1986. Changes in life-cycle strategies of *Carabus problematicus* over a range of altitudes in Northern England. Ecol. Entomol. 1: 17-26.
- COTRELL, R. G. 1936. The Biology of *Dasymutilla bioculata* Cresson. Unpublished thesis, University of Minnesota, St. Paul, Minnesota, 42 pp.
- DALY, H. V. 1961. Biological observations on *Hemihalictus lustrans*, with a description of the larva (Hymenoptera: Halictidae). J. Kansas Entomol. Soc. 34(3): 134-141.
- DEYRUP, M., AND D. MANLEY. 1986. Sex-based size variation in velvet ants (Hymenoptera: Mutillidae). Florida Entomol. 69(2): 327-335.
- EVANS, D. A., AND B. R. MILLER. 1969. A note on adult Overwintering of *Dasymutilla nigripes* in Michigan (Hymenoptera: Mutillidae). Michigan Entomol. 2(3/4): 74.
- FERGUSON, W. E. 1962. Biological characteristics of the mutillid subgenus *Photopsis* Blake and their systematic values. Univ. California Public. Entomol. 27: 1-91.
- HOUSTON, W. W. K. 1981. The life cycle and age of *Carabus glabratus* Paykull and *C. problematicus* Herbst (Col.: Carabidae) on moorland in northern England. Ecol. Entomol. 6: 263-271.
- KROMBEIN, K. V. 1979. Family Mutillidae, pp. 1276-1314. In Krombein, K. V., P. D. Hurd, D. R. Smith, and B. D. Burks [eds.]. Catalog of Hymenoptera of America North of Mexico. Vol. 2. Apocrita (Aculeata). Smithsonian Institution Press, Washington, D.C.
- MANLEY, D. F. 1991. The velvet ants (Hymenoptera: Mutillidae) of South Carolina. South Carolina Agricultural Experiment Station Tech. Bull. 1100, 55 pp.
- MANLEY, D. F., AND H. G. SPANGLER. 1983. Observations on daily activity patterns of mutillid wasps of the genus *Dasymutilla*. Jour. Georgia Entomol. Soc. 18: 234-239.
- MICKEL, C. E. 1924. An analysis of bimodal variation in size of the parasite *Dasymutilla bioculata* Cresson (Hymen.: Mutillidae). Entomol. News 35:236-242.
- MICKEL, C. E. 1936. New species and records of Nearctic mutillid wasps of the genus *Dasymutilla*. Annal. Entomol. Soc. Amer. 29(1): 1-60.
- MICKEL, C. E. 1937. The mutillid wasps of the genus *Timulla* which occur in North America north of Mexico. Entomol. Amer. 17 (n.s.): 1-119.
- POTTS, R. W. L., AND R. F. SMITH. 1944. Hibernation of *Dasymutilla aureola pacifica*. Pan-Pacific Entomol. 22(2): 60.
- WALLIN, H. 1988. Mandible wear in the carabid beetle *Pterostichus melanarius* in relation to diet and burrowing behavior. Entomol. Exp. Appl. 48: 43-50.
- ZOUHOURIAN-SAGHIRI, L., A. KOBILINSKY, Y. GILLON, AND C. GAGNEPAIN. 1983. Lois d'usure mandibulaire chez *Locusta migratoria* (Orthopt. Acrididae) son utilisation pour la datation des ailes. Ann. Soc. Entomol. France (ICS). 19(3): 335-352.