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BIOLOGY OF A WOOD-NESTING WASP, *MIMUMESA MIXTA* (W. FOX) (HYMENOPTERA: SPHECIDAE), AND ITS PARASITE, *ELAMPUS VIRIDICYANEUS* NORTON (HYMENOPTERA: CHRYSIDIDAE)

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Abstract.—An aggregation of *Mimumesa mixta* nests was located near the end of a decayed Douglas-fir timber in a second-story porch deck in Berkeley (Alameda Co.), California. Cells were excavated in the rotting wood in approximately linear series parallel to the grain and separated from one another by plugs of macerated wood fragments. Nests were provisioned with several adult and nymphal cicadellid and delphacid homopterans. Both *M. mixta* and its chrysidid parasite *Elampus viridicyaneus* Norton were reared from the nests. The sex ratio of *M. mixta* did not differ significantly from 1:1, while all emerging *E. viridicyaneus* were female. The cocoons of both wasps are described.

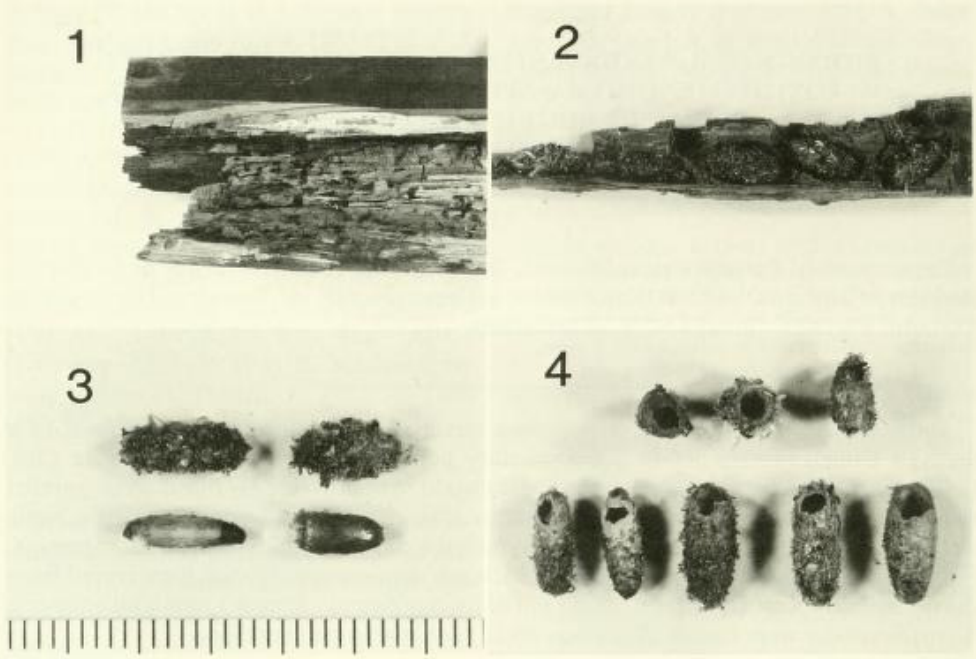
The genus *Mimumesa* (Hymenoptera: Sphecidae) is distributed throughout the Nearctic, Neotropical, Palearctic, and Oriental Regions (Bohart and Menke, 1976). These wasps excavate multicellular nests in level or sloping ground, decaying wood, and plant stems and provision them with delphacid or cicadellid prey (Bohart and Menke, 1976; Spooner, 1948; Tsuneki, 1959; Petit, 1979). Gurney (1951) provided the only description of the nesting biology of a North American species of *Mimumesa*, that of *Mimumesa nigra* (Packard). The discovery of a large aggregation of *Mimumesa mixta* (W. Fox) nests provided an opportunity to study the biology of this species as well as that of its parasite, *Elampus viridicyaneus* Norton (Hymenoptera: Chrysididae).

METHODS

The timber containing the nesting aggregation was collected in Berkeley, Alameda County, California on 15 July, 1985. To simulate natural conditions the timber was maintained in an exterior screened cage in a shaded exposure at the Oxford Agricultural Tract, University of California, Berkeley until the adult emergence occurred during May, 1986. Cell dimensions were measured to the nearest millimeter, and host and parasite cocoons were measured with a calipers accurate to 0.05 mm. Voucher specimens of both wasp species have been deposited in the R. M. Bohart Museum of Entomology, Department of Entomology, University of California, Davis.

RESULTS

Nest location and architecture.—Nests were located near one end (approximately 0.6 m) of a large timber made by glue-laminating seven Douglas-fir, *Pseudotsuga menziessi* (Mirb.) Franco, 2 × 4 (inch) boards together. The timber was found in a stack of lumber that had been removed during the previous week from a second story



Figs. 1–4. 1, *Mimumesa mixta* nesting aggregation in decayed end of a 9 × 30 cm timber. 2, Linear series of *M. mixta* cells. 3, Cocoons of *M. mixta* (left) and *Elampus viridicyaneus* (right). Cocoons pictured in upper row are intact, while those below have been sectioned lengthwise to reveal internal structure. Small divisions of scale are in mm. 4, Cocoons of *E. viridicyaneus* (above) and *M. mixta* (below), showing emergence holes. Same scale as previous figure.

porch deck. No active wasps were observed at the time of collection, the entire aggregation being composed of overwintering individuals. The timber was located between 2.5 and 4 m above ground. At the time of collection the end of the timber containing the wasp nests was dry but already decayed by brown-rot fungi (Basidiomycetes). *M. mixta* was apparently able to excavate the decay-softened wood.

The nest aggregation consisted of over 400 cells which extended throughout the decayed portion of the timber but not into the sound wood (Fig. 1). Cells were arranged end to end in approximately linear series parallel to the grain (Fig. 2), each being separated from the next by a plug of macerated wood fragments. Nests appeared to be interconnected, and we were unable to determine where an individual nest began or ended. Measurements of 30 randomly selected cells gave a mean cell length of 9.3 ± 1.8 mm and mean width of 4.0 ± 0.6 mm (range 5–12 mm by 3–5 mm). No cell contained more than a single cocoon.

Host and parasite populations.—After adult emergence the wood was dissected to provide an estimate of the sizes of the host and parasite populations (Table 1). A total of 44 *M. mixta* emerged successfully. An additional 119 *M. mixta* larvae, pupae, and adults were found inside cocoons; some of these were alive, and it is unclear to what extent additional emergence might have occurred. Two host cocoons, one containing a dismembered adult wasp and the other a mass of insect frass, had apparently been attacked by fly larvae of the family Sciari-

Table 1. No. of specimens of *Mimumesa mixta* and *Elampus viridicyaneus* reared or dissected from a nesting aggregation.

Species and Stage	No.
Mimumesa mixta	
Emerged adults ♀	19
♂	25
Pupae/adults within cocoons ♀	33
♂	31
Pupae within cocoons, unsexable[1]	12
Larvae within cocoons	43
Emerged cocoons	131
Cocoons with fly feeding holes only	2
Elampus viridicyaneus	
Emerged adults ♀	22
♂	0
Pupae/adults within cocoons ♀	12
♂	0
Pupae within cocoons, unsexable[1]	5
Larvae within cocoons	18
Emerged cocoons	192
Cocoons with fly feeding holes only	3

[1] Pupae that died before sclerotization.

Table 2. Species of Homoptera recovered from cells of *Mimumesa mixta*.

Taxon	No. Adults/Nymphs
Delphacidae	
Delphacodes sp.	1 adult
Cicadellidae	
Sorhoanus helvinus (Van Duzee)	59 adults
Tiaja californica (Ball)	8 adults
Euscelidius variegatus (Kirshbaum)	8 adults
Amblysellus grex (Oman)	5 adults
Endria lassus (Ball)	2 adults
Calanana rubralineata (Beamer)	1 adult
Reticopsis nubila (Van Duzee)	1 adult
Deltocephalinae, undetermined	10 adults
Deltocephalinae, undetermined	5 nymphs

dae, which left a single, small (ca. 0.7 mm diameter), irregular hole in each cocoon. These fly larvae were common throughout the nest aggregation and appeared primarily to be fungivores, only incidentally attacking cocoons. The sexes of 63 of the sphecid pupae could be determined, which when combined with the data from the adults yielded a sex-ratio of 52 females : 56 males or 1: 1.08, which was not significantly different from 1:1 ($z = -0.39$, $P > 0.5$). The 131 host cocoons with emergence holes exceeded the number of emerged adults by 87, indicating that some of the cocoons may have remained from one or more previous generations.

Twenty-two adult *E. viridicyaneus* emerged successfully. Twenty-five larvae, pupae, and adults were found inside cocoons; some of these appeared to be alive and might have emerged later. Three empty parasite cocoons had apparently been attacked by fly larvae. The 22 adults and 12 pupae whose sex could be determined were all females. Barring strongly sex-specific mortality in the immature stages, *E. viridicyaneus* showed a female-biased sex ratio ($z = 5.8$, $P < 0.001$). The 192 *E. viridicyaneus* cocoons with normal emergence holes exceeded the number of observed emerged adults, suggesting the existence of one or more earlier generations of parasites in the same nesting aggregation.

Nest provisions.—*M. mixta* provisioned cells with adult and nymphal Homoptera (Table 2). Nine species of cicadellids and one delphacid were recovered; 59 of the 100 prey individuals recovered represented a single species of cicadellid, *Sorhoanus helvinus* (Van Duzee). Intact prey were found both in cells in which the wasp larva had died and in cells containing cocoons. Two apparently complete cells contained 18 and 19 prey items, respectively.

Mimumesa mixta cocoons.—Cocoons of *M. mixta* (Figs. 3, 4) were oblong, spongy in texture, and generally covered with wood and fragments of devoured provisions. Cocoons averaged 8.5 ± 0.7 mm long by 3.3 ± 0.3 mm wide (range 6.7–9.7 mm by 2.8–3.8 mm, n = 60). The inner surface of the cocoon was light brown and very smooth;

the end opposite that with the generally off-center exist hole was coated thinly with the dark brown meconium.

Elampus viridicyaneus cocoons.—Cocoons of *E. viridicyaneus* (Figs. 3, 4) were superficially similar to those of *M. mixta*, being oblong and covered with wood fragments and prey debris. However, they were shorter, and the cocoon walls were crisp, paper-like, and had a varnished appearance. The inner cocoon surface was darker than that of *M. mixta* and was roughly textured. The exit hole was centered and represented the removal of the end of the cocoon. Mean cocoon dimensions were 6.7 ± 0.8 mm long by 3.2 ± 0.2 mm wide (range 4.9–9.0 mm by 2.6–3.88 mm, n = 42).

Discussion

Mimumesa mixta.—Several *Mimumesa* species are known to nest in the soil, and *Mimumesa dahlbomi* (Wesmael), *Mimumesa dahlbomi pacifica* (Tsuneki), and *Mimumesa nigra* (Packard) are known to nest in decayed wood (Bohart and Menke, 1976; Spooner, 1948; Tsuneki, 1959; Petit, 1979). Spooner (1948) suggested that *Mimumesa unicolor* (Vander Linden) and *Mimumesa littoralis* (Bondroit) (as *Mimesa celtica* Spooner) may nest in plant stems, but *M. unicolor* has subsequently been found nesting in the ground (Petit, 1979) and the biology of *M. littoralis* has not been described. The short description by Gurney (1951) of a *M. nigra* nest is the only description of the biology of a North American species.

Gurney (1951) reared a single *M. nigra* male from a cocoon taken from a nest containing "a dozen or more cells" in the decayed end of a 2 × 4 (inch) fence board ca. 30 cm above ground. Although abandoned beetle borings are used by *M. dahlbomi* and *M. dahlbomi pacifica* to gain entry into the wood (Bohart and Menke, 1976; Spooner, 1948; Tsuneki, 1959), Gurney (1951) did not mention any evidence of beetle infestation in the board containing the *M. nigra* nest. Likewise, we found no evidence of wood-boring beetle activity in the timber containing the *M. mixta* nests. *M. mixta* may either have excavated directly into the soft, decayed end-grain of the board or entered through cracks in the decayed wood. Species of the genus *Psen*, the only other genus in the subtribe Psenina known to nest in decayed wood (Bohart and Menke, 1976), apparently excavate directly into stumps (Iwata, 1938; Tsuneki, 1959).

The number of empty host and parasite cocoons exceeded the number of newly emerged adults, suggesting that both *M. mixta* and its parasite were active at the nesting site for one or more previous generations. The complete history of the nesting aggregation cannot, however, be inferred from our single collection due to the possible re-use of old cells by *M. mixta*.

Mimumesa unicolor, the only *Mimumesa* species known to be attacked by chrysidid parasites, has been reported as a host of *Chrysis succincta* L., *Hedychridium ardens* Cocquebert, and *Omalus auratus* (L.) (Bohart and Menke, 1976; Móczár, 1967; Spooner, 1948).

Elampus viridicyaneus.—The genus *Elampus* contains six species in North America (Bohart and Kimsey, 1982) for which the biology is almost completely unknown (Huber and Pengelly, 1977). The only published host record for a North American species is for *E. viridicyaneus* parasitizing *Hoplisoides costalis* (Cresson) (as *Psammaecius costalis* (Cr.)) (Krombein, 1958). Huber and Pengelly (1977) relate that this record is based upon a single specimen in the U.S. National Museum bearing the label "Bred from nests of *Gorytes* (s.l.) from Huntington, L.I. Cocoon March 24, 1924. em. April 30, 1924. S. C. Bridwell." *Hoplisoides costalis* is a ground-nesting, membracid-provisioning nyssonine (Evans, 1966), while *M. mixta*, as presented above, nests in decaying wood, provisions with cicadellids and delphacids, and is in the subfamily Pemphredoninae. Thus Krombein's (1958) record combined with that presented here im-

plies a host range for *E. viridicyaneus* that is broad in both the systematic and behavioral/ecological senses. Observations of sand grains trapped in the coarse integumentary punctations of curated specimens of *Elampus* spp. (Huber and Pengelly, 1977; Kurczewski and Kurczewski, 1970) support the suggestion that the host pool of North American *Elampus* spp. includes at least some ground-nesting species. Spooner (1948), summarizing the European literature, and Móczár (1967) together listed three species in the genus *Mimesa* as hosts of two European *Elampus* species. These three *Mimesa* species, and indeed all the members of the genus for which biological information exists, construct nests in the ground (Bohart and Menke, 1976). Thus, worldwide, the genus *Elampus* does parasitize both wasps that excavate nests in rotting wood and wasps that nest in the ground. The genus *Mimesa* is closely related to *Mimumesa,* both being members of the subtribe Psenina (Bohart and Menke, 1976).

The significance of the female-biased sex ratio of emerging *E. viridicyaneus* is unclear. Museum collections of this and other *Elampus* species generally include approximately equal numbers of both sexes (Bohart and Kimsey, 1982; Huber and Pengelly, 1977). Highly female-biased sex-ratios for single batch rearings of chrysidid parasites are not uncommon (e.g. Krombein, 1967; Medler, 1964) and sex ratios may vary between sites (Krombein, 1967).

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