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ETHOLOGY AND OVERWINTERING OF *PODALONIA LUCTUOSA* (HYMENOPTERA: SPHECIDAE)[1]

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ABSTRACT

The nesting and overwintering behavior of *Podalonia luctuosa* (Smith) was studied in New York and Colorado. Females provisioned shallow (ca. 2 cm deep), unicellular nests with a single cutworm (Noctuidae) during April, May, and July. Paralyzed prey were transported on the ground and were cached on plants just above ground level. Prey weights averaged about 400 mg. The miltogrammine fly *Hilarella hilarella* Zetterstedt parasitized prey at both localities. From 1 to 10 adult females were found to overwinter in burrows 0.5 m deep, which were dug in late summer and early fall. Collection data and field studies indicated that *P. luctuosa* is bivoltine in the NE U.S.

Wasps in the genus *Podalonia* occur in the major temperate and tropical areas of the world, except South America. There are 66 species world-wide, of which 20 are found in North America (Bohart and Menke 1976). *Podalonia* is a member of the tribe Ammophilini, and is closely related to the genus *Ammophila*.

Murray (1940) revised the key to the North American species of *Podalonia*, of which most are found west of the 100th meridian. Prior to Murray's revision, the species were poorly characterized and confused due to Fernald's (1927) revision and his (subsequent) wrong ideas of speciation within the genus (Bequaert 1929, Fernald 1931). Early accounts of *Podalonia* behavior may, therefore, have involved more than one species. Newcomer's (1930) and Hicks' (1931a, 1931b, 1932) papers on *P. luctuosa* (Smith), for example, probably included observations on *P. communis* (Cresson) (Murray 1940, Bohart and Menke 1976, Krombein 1979), and must be treated as containing information on both species.

The Ammophilini prey upon lepidopterous larvae, *Podalonia* taking soil-inhabiting noctuids (cutworms) which are often agricultural pests, and *Ammophila* preying primarily on plant-inhabitors of various families (Evans 1959, Bohart and Menke 1963, Evans and Eberhard 1970). Bohart and Menke (1976) have summarized the ethology and systematics of *Podalonia*.

Although *Podalonia* preys primarily on cutworms, several species in the genus deviate from this preference. *P. occidentalis* Murray has been noted preying on tent caterpillars (Lasiocampidae) in New Mexico (Murray 1940); *P. valida* (Cresson) upon the arctiid *Estigmene acrea* (Drury) in Arizona (Steiner 1974); and *P. hirsuta* Scopoli utilizing gypsy moth larvae (*Lymantria dispar* (L.)) in Europe (Roth 1928). These cases are unusual because the wasps preyed upon extremely hairy, arboreal lepidopterans.

Podalonia exhibits somewhat primitive behavior for a sphecoid in that it digs a nest after capturing prey, a trait common to the Pompilidae. The Asiatic *P. nigrohirta* (Kohl) is an exception, being the only species known to prepare a burrow prior to hunting for prey (Tsuneki 1968).

The behavior of the North American species of *Podalonia* has been only sporadically noted. Aldrich (1891) and Krombein (1936) reported briefly on the behavior of *P. robusta*

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(Cresson) (misdet. as *P. violaceipennis* (Lepeletier)). Hicks (1933) noted the nesting behavior and parasitism of *P. sericea* Murray (misdet. as *P. violaceipennis*) in California, and Evans (1963a, 1970) described the nesting of this species at Jackson Hole, Wyoming. Steiner (1974, 1975) reported *P. valida* preying upon Arctiidae and described female territoriality in Arizona. Parker (1915) and Balduf (1936) recorded aspects of the nesting behavior of *P. violaceipennis*. A brief note on *P. communis* nesting at Jackson Hole, Wyoming, was published by Evans (1970).

P. luctuosa occurs transcontinentally in the northern and montane regions of North America, ranging as far north as the Yukon (Steiner 1973, Krombein 1979). In the western U.S. (i.e., west of 100th meridian), it is sympatric with the almost indistinguishable *P. communis*, and was confused with it in the early literature. (In the east, *P. communis* does not occur. This at once suggests an advantage for field study of *P. luctuosa* there.) Newcomer (1930) reported on prey cachement, nest excavation, closure, egg placement, prey, predators, and parasites of "*P. luctuosa*" at Yakima, Washington. He found some wasps abandoning small prey, and others stealing from conspecifics. Hicks (1931a, 1931b, 1932) observed "*P. luctuosa*" nesting in Colorado and California and noted hunting, prey capture, nesting, and pre-overwintering behavior. Wasps took prey that had been parasitized by *Meteorus vulgaris* Cresson (Ichneumonidae) and *Wagneria carbonaria* Panzer (Tachinidae) prior to capture. Evans (1970) found *Philanthus zebratus nitens* (Banks) preying upon *P. luctuosa* males in Wyoming.

This report extends the study of *P. luctuosa* to the eastern U.S. and adds new information on life history and behavior, both for this region and generally.

STUDY AREAS

P. luctuosa was studied near Mallory, Oswego County, New York, during 1979–1981, and at the Great Sand Dunes National Monument, Alamosa County, Colorado, on 24 May 1980. One observation made at the St. Anthony Sand Dunes, Fremont County, Idaho, on 22 June 1979 by N. B. Elliott is included.

Observations were made at two Mallory sites: flat and inclined areas of open and moss-covered sand, and sandy and gravelly slopes bordered by a woods, field, and road (Mallory I); and a recently bulldozed flat area of fine sand bordered by a hedgerow, road, woods, and field (Mallory II) (Fig. 1). The sparsely vegetated areas contained scattered grasses, milkweed (*Asclepias* sp.), St. John's-wort (*Hypericum* sp.), and cinquefoil (*Potentilla recta*). Moderate vegetation covered most of the sand, with grass clumps, clover patches, *Erigeron*, and other forbs dominating. Heavily vegetated areas were covered with Queen Anne's lace (*Daucus carota*), goldenrod (*Solidago* spp.), timothy grass (*Phlaeum pratense*), clovers (*Melilotus alba, Trifolium* spp.), and other plants. Most observations were conducted at Mallory II because of the large population of wasps found there.

FEMALE ACTIVITY

At Mallory, New York, *P. luctuosa* females were active from 20 April to 17 October, during sunny to partly cloudy days at ambient temperatures of from 15° to 34°C, and surface temperatures of from 23.5° to 54°C from 0830 to 1730 (EDT). Three seasonal periods of activity were evident: April to late May, July, and August to October.

Sun-basking occurred frequently in early spring and late fall during cool days. Wasps flattened themselves against the sand with legs extended, and remained motionless for up to 30 sec. They then groomed themselves, or resumed other activities. This behavior was not evident when ambient temperatures were above 20°C.

P. luctuosa females constructed and utilized resting burrows for the night and periods of inclement weather. Two females brought into the laboratory and confined in a 20-gallon aquarium dug shallow burrows in sand for the night. On 21 April at an ambient temperature of 15°C, one female was seen excavating a burrow in a sandy, moss-covered slope. After

Figs. 1–2. (1) Sandpit (Mallory, NY) where *Podalonia luctuosa* nested in May 1979. (2) Female *P. luctuosa* examining her cached prey (*Nephalodes minians*) on a cinquefoil (*Potentilla recta*) at Mallory, NY. (Photograph by R. A. Norton.)

removing five loads of soil, she retreated into the burrow. Ten min later, the burrow was excavated with the wasp inside. The sloping burrow, 8 mm wide, 7 cm long, and 5 cm deep, had a 3 by 8 cm tumulus adjacent to the entrance.

Females took nectar from flowers nearby, feeding mainly on *Berberis vulgaris* in the spring and various Asteraceae during summer and fall. *P. luctuosa* females released a strong "phenolic" odor when they were handled, possibly from a defensive secretion.

HUNTING BEHAVIOR AND PREY CAPTURE

P. luctuosa females were observed inspecting grass tufts, bases of plants, and depressions, running along with their head to the ground, tapping the antennae against the substrate. Females circled in certain areas, particularly near clumps of grass or plant bases. One wasp tapped her antennae on the ground in an area where another had left a cutworm several minutes earlier; she then circled and moved away.

At Mallory II hunting was concentrated in the sparsely to moderately vegetated areas. Searching wasps rarely visited heavily vegetated (old field) areas or bare sand. Some females ranged over 150 m^2 within 15 min, while others confined their searching to a 10-m^2 area during the same time period.

When sand temperatures reached 32°C, females made short flights from plant to plant in search of prey. In July, at higher temperatures, females searched in shaded areas beneath overhanging vegetation rather than in open areas. Periodically, females stopped searching and fed on nectar.

While digging for prey, females exhibited antennal tapping, wing buzzing, and scraped away soil with their mandibles and forelegs. If rootlets, small sticks or other debris were encountered while digging, the wasp would either remove the obstacle or dig from another angle. Unsuccessful wasps stopped digging and resumed hunting elsewhere. After two wasps had stopped digging, their excavations were examined. A large dipterous larva was found at the bottom of one cavity, a small spider in the other.

When a cutworm was encountered, the wasp attempted to dig around it to facilitate its removal from the ground. Some cutworms tried to escape or defend themselves. Cutworms on the ground tried crawling away. One cutworm crawled up a plant stem and another curled its body, moving back and forth when the wasp tried to grab it, but neither escape nor defense was successful.

Prey were stung in their venters, starting at the anterior and progressing to the posterior end. Females were observed to sting prey two to six times in the thoracic segments, one to four times in the abdominal segments, and once or twice in the anal proleg segment. If the cutworm was still moving, it was stung in the moving area, usually near the anal prolegs, as these grasped onto vegetation and made transport difficult.

Females malaxated the cervical region and, sometimes, the midsection of the cutworm after administering the initial stings to the thorax. In one case, a wasp stung the prey in the midsection as it was trying to climb up a grass stem. She stung the cutworm four to six times more in the thorax, malaxated the prey just behind the head, stung the anal segment, and malaxated at several points along the length of the body. The wasp examined the prey for several seconds, and then malaxated it once more behind the head. Prey were not carried to a cache until they were completely immobilized.

PREY CACHING

P. luctuosa females (24) cached their paralyzed prey on a grass blade, leaf, or branch, often near where they obtained it (Fig. 2). They began digging a nest within 2 m of this site, except for four wasps which carried their cutworms 6, 12, 15, and 20 m, respectively, before finding a suitable storage site. Prey (19) were placed an average of 4.1 ± 2.4 cm ($\bar{x}$ ± SD) above the ground (range 0–10 cm). Prey were stored on grasses 52% of the time; on other plants or sticks, 40%; and on the ground, 8%. Females examined their prey after placing it at the site and sometimes repositioned the cutworm before leaving to dig the burrow.

BURROW CONSTRUCTION

P. luctuosa females searched for suitable nesting sites on flat, sloping, or moss-covered areas of sand, digging at one location, then another. Females (10) made 2–15 attempts at burrow excavation before remaining in one place. Wasps initiated burrows by scraping in unison with the forelegs and biting at the soil, then throwing it backwards beneath the body with the forelegs. Females possess a basket-like structure of long stiff hairs beneath the head and on the forefemur, called a psammophore or "sand-basket" (Bohart and Menke 1963), that enables them to carry sand from the burrow. Wasps carried out sand with the psammophore, and deposited it a few centimeters from the entrance. After depositing two to four loads, a female raked sand away from the entrance, creating a low, fan-shaped tumulus. Much wing buzzing accompanied the digging activities. Females (13) took 6–20 minutes ($\bar{x}$ =

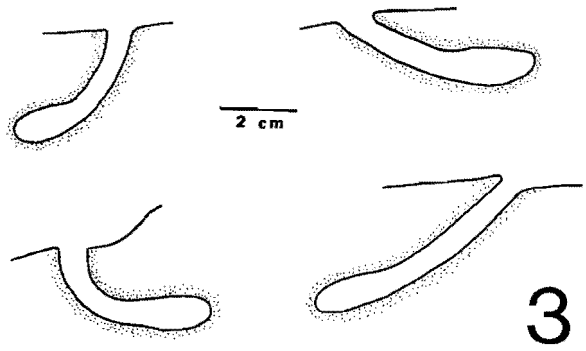


Fig. 3. Side views of *P. luctuosa* nests (Scale refers to all nests.)

10.15 ± 4.12) to excavate a nest. Some wasps stopped digging momentarily to examine their prey or to rest and groom, accounting for the longer excavation times.

Nests (28) comprised simple, unicellular burrows which usually sloped downward; a few were nearly vertical (Fig. 3). The cells comprised terminal enlargements, angling away from the burrow shafts. Entrances were approximately circular, ranging from 6 to 11 mm in diameter ($\bar{x}$ = 8.2 ± 1.16 mm). The burrows had a mean length of 2.3 ± 0.5 cm (range 1.0–3.2 cm), with the cells varying from 1.0 to 3.0 cm deep ($\bar{x}$ = 1.9 ± 0.5 cm). Cells were ovoidal when viewed from above. They ranged in length from 1.0 to 2.9 cm ($\bar{x}$ = 1.6 ±0.4 cm), and in width from 0.8 to 1.3 cm ($\bar{x}$ = 1.0 ± 0.2 cm). Significant differences in nest dimensions between the spring nesting and the midsummer generations of wasps were not apparent (*t* test, $P > 0.05$).

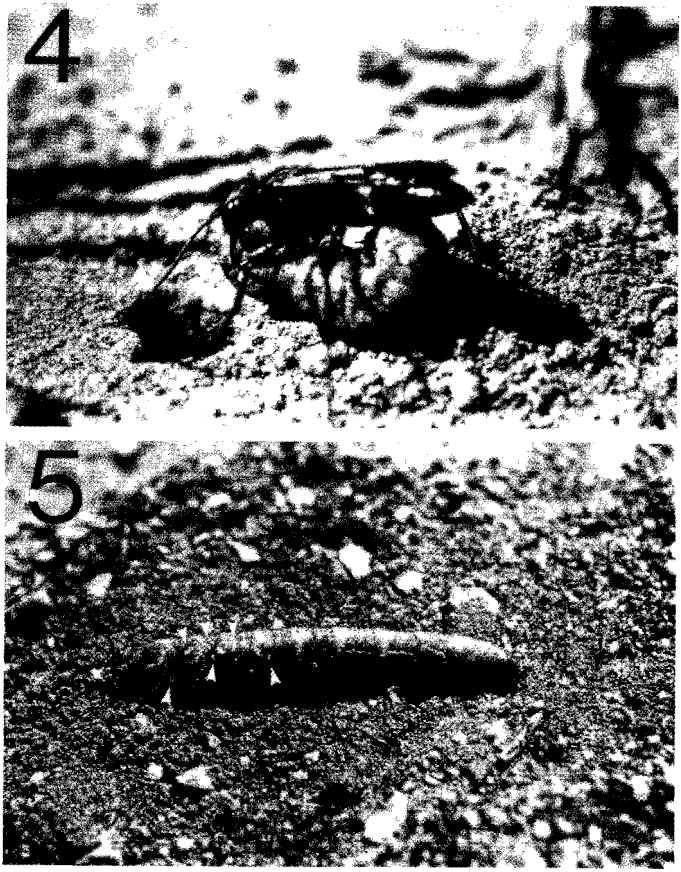
Females stopped digging temporarily and rested on nearby vegetation when the surface temperature exceeded 40°C. Wasps assumed a characteristic position, as they grasped a grass stem and faced downward away from direct sunlight, 10–30 cm above the sand. This position was held for 20 to 30 sec; then the wasps returned to dig or close the nest. Some individuals repeated this behavior several times in succession.

When a wasp had finished excavating her burrow, she backed out, groomed briefly, examined the entrance, and often reentered to remove another load of sand. Wasps did not come out head first, upon completion, as do many Pompilidae.

ORIENTATION AND PREY TRANSPORT

Orientation to the nest consisted of the wasp making concentric zigzagging paths on the ground around the entrance, and ended with her walking toward the prey. *P. luctuosa* usually went directly to the cache, although some individuals spent up to 5 min locating their prey. Wasps (16) carried their prey a mean distance of 1.64 m (range 0.3–7 m) from the cache to the nest.

Wasps grasped prey venter-up, just behind the head, in the thoracic region with the mandibles and forelegs, respectively (Fig. 4). Prey were dragged forward to the nest in a more or less straight line. Wasps often paused to examine their prey and groom themselves enroute to the nest. If a wasp had difficulty in finding her nest, she left the prey in a clump of grass, reoriented, retrieved the prey, and then proceeded to the nest. The time spent in transporting prey to the nest ranged from 0.5 to 7 min ($\bar{x}$ = 2.5, n = 16). The prey was then released at the entrance. The wasp entered her burrow, turned around within, reappeared at the entrance, and pulled the cutworm inside headfirst with her mandibles.



Figs. 4–5. (4) Female *P. luctuosa* transporting cutworm to her nest. (Photograph by R. A. Norton.) (5) *Hilarella hilarella* maggots (arrows) on a *Euxoa* sp. cutworm. (Photograph by R. A. Norton.)

FINAL CLOSURE

Wasps (21) spent from 20 to 120 sec ($\bar{x}$ = 52 ± 23.4 sec) inside the burrow for prey positioning and oviposition, then emerged head first and started scraping sand from the walls of the burrow. Females threw sand from the tumulus into the burrow with the forelegs and packed it in with the head, accompanied by frequent wing vibration. Pieces of plant debris, small stones, sticks, and fecal pellets were often used to fill the last few millimeters of the burrow, and were sometimes pounded into the fill with the head or scattered over the entrance area. A final raking obliterated any traces of the entrance, followed by an inspection of the nest area. The wasps then flew straight up, hovered approximately 15 cm over the nest, and flew away. Nest closure ranged from 2 to 10 min ($\bar{x}$ = 5.2 ± 2.3 min; n = 19).

Table 1. *Podalonia luctuosa* prey records.

Species of Noctuidae	Number of Records	Source
Agrotis sp.	4	Colorado
Aletia oxygala (Grote)	1	New York
Chorizagrotis agrestris Grote	—	(Hicks 1932)
Euxoa sp.	1	Colorado
Graphiphora badinodis (Grote)	1	New York
Lacinipolia sp.	2	New York
Leucania commoides Guenée	4	New York
Lycophotia margaritosa Haworth	—	(Hicks 1932)
Lycophotia saucia Hübner	—	(Hicks 1932)
Nephalodes minians Guenée	2	New York
Sunira bicolorago (Guenée)	1	New York
Noctuidae spp.	—	(Newcomer 1930)
Agrotinae spp.	5	New York, Idaho
Trifid Noctuidae (10 species groups)	16	New York

PREY

P. luctuosa preyed exclusively on soil-inhabiting noctuid larvae (cutworms) (Table 1). (Cutworms feed on plants on the surface at night, and retreat to underground burrows during the day.) Identification of many larval Noctuidae is difficult because they have not been associated with the adult (T. McCabe, pers. comm.). Hence, many of the prey obtained in this study were identified only to subfamily or tribe. Wasps nesting in the spring at Mallory preyed upon cutworms that had overwintered as larvae, whereas different species of cutworms were utilized in July.

Prey weights (26) ranged from 209 to 880 mg ($\bar{x}$ = 396 ± 138 mg). Two female wasps weighed 54 and 86 mg, for a 3 to 6:1 prey to wasp weight ratio.

PREDATORS AND PARASITES

Adult tiger-beetles *Cicindela scutellaris* Haldeman and *C. repanda* Dejean were seen stalking wasps digging burrows and carrying prey at Mallory. *P. luctuosa* females responded by chasing away or fighting with the beetle. Tiger-beetles were never successful in capturing adult wasps, but were twice found sucking juices from paralyzed cutworms, apparently after a wasp had dropped its prey.

At the Great Sand Dunes National Monument, one *P. luctuosa* female abandoned her prey when 10 to 15 *Formica bradleyi* Wheeler (Formicidae) started attacking the cutworm. The wasp landed near the prey, buzzed her wings, hovered above the prey, and flew off. At Mallory II, several *Formica* sp. were observed carrying away a cutworm after the wasp had abandoned it.

Two *P. luctuosa* males were seen being eaten by the crab-spider, *Misumena vatia* Clerck, on *Daucus carota* flowers.

No parasites were recovered from the nests of *P. luctuosa* or observed in the vicinity of the nests during April and May at Mallory. In contrast, females nesting at Mallory during July were often trailed by satellite-flies (Sarcophagidae: Miltogrammini).

Miltogrammine flies were numerous in late May at the Great Sand Dunes National Monument. From one to six flies followed females as they searched for prey and trailing intensified when wasps were carrying prey to the nest. Several *Hilarella hilarella* Zetterstedt larviposited on a *Euxoa* sp., as it was being dragged into a burrow. Subsequent excavation and examination of this prey revealed nine fly larvae on the cutworm, several of which had

already destroyed the wasp's egg (Fig. 5). At the St. Anthony Sand Dunes, Idaho, several *Senotainia rubriventris* Macquart (Sarcophagidae) were observed trailing a *P. luctuosa* female carrying prey.

At Mallory, prey that had been cached on plants were never approached by satellite flies. When the wasps were digging burrows, satellite flies perched on nearby plants. *H. hilarella* followed females with prey at distances of from 1 to 10 cm. When the wasp left the cutworm at the entrance to the burrow, prior to pulling it within, the miltogrammines larviposited on the exposed prey, and two flies once larviposited simultaneously.

When *P. luctuosa* females encountered satellite flies, they lunged at them while buzzing their wings and elevating their body. Wasps did not seem to differentiate between prey which had or had not been parasitized, nor was there cleaning of the prey or prey abandonment due to parasites.

Five of ten nests excavated in July were parasitized by miltogrammine flies. From two to seven maggots were found in four nests, with the wasp's egg being eaten or having already been destroyed by maggots. Two parasitized prey were brought indoors for rearing on 7 July. Seventeen days later, seven *H. hilarella* emerged from one cutworm and two *H. hilarella* from another.

DEVELOPMENT AND ECLOSION

Eggs (27) of *P. luctuosa* were placed on the left (70.3%) or right (29.7%) sides of the prey. Eggs were located on the first (3.7%), second (18.5%), third (63%), fourth (11.1%), or fifth (3.7%) abdominal segment. They were always attached to the abdominal midline of the prey by the anterior end, the posterior end curving ventrally away from the body. Iwata (1976) termed this type of egg placement the "*Ammophila* type." The eggs varied from 2.0 to 2.7 mm long by 0.3 to 0.4 mm wide.

The larval development of *Podalonia* had been described by Parker (1915), Newcomer (1930), and Hicks (1932). One prey bearing a *P. luctuosa* egg was brought into the laboratory on 21 April and placed in a rearing tin. On 25 April, a first instar larva was visible through the egg chorion, and the cutworm had voided its gut contents. This larva grew to 5 mm in length and was feeding actively on 28 April. It had consumed the majority of the inside contents of the prey by 30 April, and was neary full-grown. Twenty-four h later the larva had consumed everything but the cutworm's head capsule. The larva started spinning a cocoon on 3 May, but died a few days later.

A cutworm bearing an egg was placed in a sand-filled pot on 9 July and by 20 July the wasp larva had spun a cocoon. A male eclosed from this cocoon on 2 August. The ovoidal cocoon measured 18 by 6 mm and consisted of an outer layer of sand intertwined with loose strands of silk and an inner layer of brown, semi-transparent silk.

MALE ACTIVITY

Males were active from 21 June to 20 August, between 0830 to 1600 (EDT) at Mallory II on sunny days at ambient temperatures of from 22° to 34°C. They fed upon the nectar of various flowers, especially *Erigeron canadensis, Chrysanthemum leucanthemum,* and *Lepidium virginicum*. Males flew 2 to 20 cm above the ground in long, looping flights, stopping frequently to feed on nectar, or to inspect clumps of grass, low growths of weeds, and depressions in the ground.

Interaction with other males or insects prior to the emergence of the females were few. Once females emerged, conspecific interactions were frequent. Three kinds of interactions between males were observed in the field. Twice, one male landed on a flower while another was feeding there. The resident male drove off the intruder and resumed feeding. Twice, one male attempted copulation with another male by pouncing on it from the air. Both males grappled on the ground, with one flying away and the other remaining. Four times one male trailed behind another in flight. When the leading male located a female *P. luctuosa* and

attempted to mate, the trailing male did likewise, resulting in all three wasps tumbling on the ground. Both males were apparently unsuccessful in mating.

Two types of male-female interactions were observed. Five times males landed within several centimeters of females and advanced toward them. The females responded by assuming a threat posture, spreading their wings, opening their mandibles, and lunging at the males, causing them to retreat and fly away. All females had been hunting prior to being disturbed. The second type of interaction between males and females resulted when a male flew atop a stationary female and attempted copulation. The pair tumbled on the ground and separated within 10 sec, an apparently unsuccessful mating. Females feeding on flowers rejected males by assuming a threat display, but did not lunge at them. Males and females often fed on flowers in close proximity (10–50 cm) on hot days during 1200 to 1400 (EDT) without interaction.

To ascertain male longevity, 31 individuals were marked at Mallory II during a two-week period in 1980. Some lived at least 25 days after being marked; others were not recaptured after a week.

OVERWINTERING

Overwintering or hibernation of adult solitary wasps appears to be restricted to females. The Palaearctic pompilids *Anopilus viaticus* (L.), *Priocnemis perturbator* (Harris), *P. coriaceous* (Dahlbom), *P. propinqua* (Lepeletier), and *Dipogon intermedia* (Dahlbom) are known to overwinter (Richards and Hamm 1939). Evans (1970) suggested overwintering for the Nearctic pompilid *Anoplius tenebrosus* (Cresson), and this was proven in New York by Alm (1979). Overwintering in the Sphecidae has been observed only in the genera *Liris* and *Podalonia*. O'Brien and Kurczewski (1982) found the larrine *Liris argentata* overwintering in New York.

Podalonia hirsuta females have been found to assemble in clusters of hundreds of individuals in rock crevices and other protected situations in the mountains of southern Europe in the fall (Roth 1928, Grandi 1961). Maneval (1939) proved that females overwintered in aggregations by marking them in the fall and recapturing them in the spring. Hicks (1931a) suspected that *P. luctuosa* overwintered upon finding a female entering a 9 by 170-mm burrow at the base of a mound of sand in Colorado during September. Four female wasps were unearthed at the bottom of the nearly vertical burrow. Large numbers of *P. communis* were found clustered under loose bark during a thunderstorm in the mountains of California (Bohart and Menke 1976).

Early spring and late fall appearances of *P. luctuosa* at Mallory suggested that these wasps overwinter. To see if collection records would reflect this, several hundred specimens were examined from the Cornell University, New York State Museum, Museum of Comparative Zoology, U.S. National Museum, and the State University of New York College of Environmental Science and Forestry insect collections, for collection dates, localities, and amount of wing fray.

Wing fray usually reflects a wasp's activities and is a rough indicator of age. Heavily frayed wings reflect a lengthy and intense period of activity; no wing fray indicates a recently emerged or inactive individual. Wing fray was categorized as none to slight, or moderate to heavy (Fig. 6). Specimens throughout the range of *P. luctuosa* were used in the wing fray analysis and in plotting the collection dates (Fig. 7).

Females were active from April to October (Fig. 7). Females collected in early spring exhibited little or no wing fray, whereas some individuals collected in late spring and early summer showed heavy wing fray, presumably associated with nesting activities (Fig. 6). During July and August, females' wings were mostly unfrayed, and in September and October the non-nesting females exhibited no wing fray (Fig. 6). Males at Mallory showed an increased amount of wing fraying and decline in their numbers as the summer progressed (Fig. 6). The absence of males in the spring and late fall is consistent with the hypothesis that only inseminated females overwinter.

Of nine females marked with paint at Mallory in late August and early September 1979,

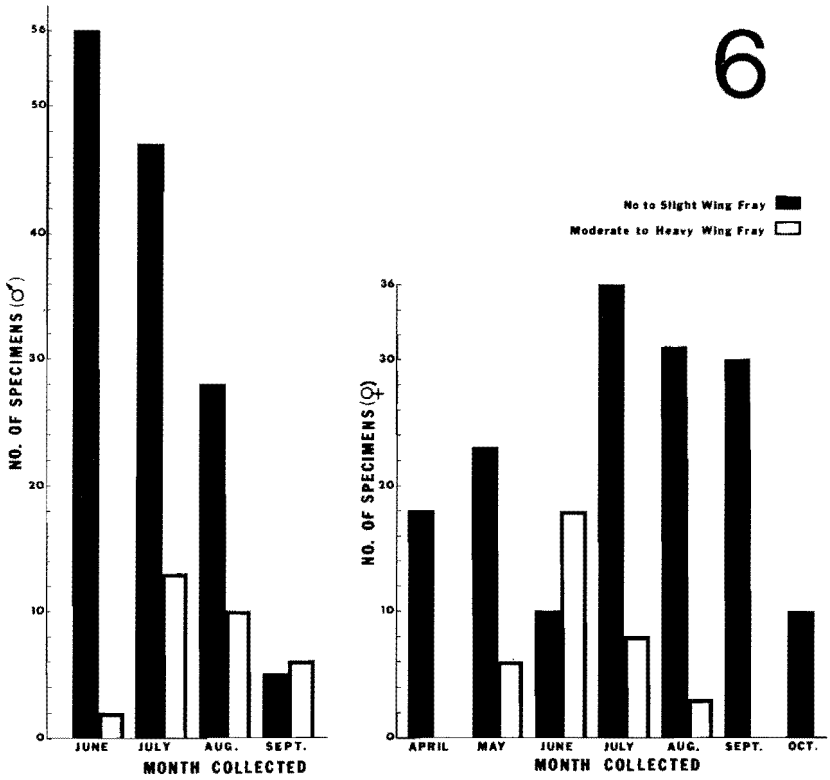


Fig. 6. Wing fray of *P. luctuosa* females and males, based upon museum specimens.

and eight females in September and October 1980, three were recaptured on 21–23 April 1980, and five on 27 April 1981, respectively, confirming overwintering.

In 1980, females (21) at Mallory were observed digging or expanding overwintering burrows between 5 August and 17 October during periods of warm, sunny weather. Each burrow entrance was usually at the base of a mound of sand, often moss-covered, and had a fan-shaped tumulus prefacing the entrance (Fig. 8). Burrow entrances invariably faced the south or southwest.

A burrow marked on 22 September, was excavated on 17 October. Although it was 23°C and sunny at the time, most herbaceous vegetation had been killed by frosts. The wasp was seen emerging from the burrow at 1400. A 6 by 9-cm weathered tumulus indicated no recent soil removal. The entrance, 9 mm in diameter, extended a short distance laterally, and the burrow, 8 mm by 26.8 cm, plunged nearly vertically downward.

On 16 November, another burrow was excavated during freezing weather. A female *P. luctuosa* was found at the bottom of an 8 mm by 52.5 cm-long burrow. The wasp was found facing head outward in torpor. The temperature at the bottom of the burrow was 5°C, the ambient temperature 6°C.

On 17 November, four overwintering burrows were excavated. The air temperature was 2°C, and the ground was frozen to a depth of 5 cm. The temperature at the bottom of all burrows was 4°C. The nearly vertical burrows were approximately 8 to 9 mm in diameter, and ranged from 44.5 to 54.6 cm long ($\bar{x}$ = 49.9 cm) and 44 to 48.3 cm deep ($\bar{x}$ = 46.3 cm)

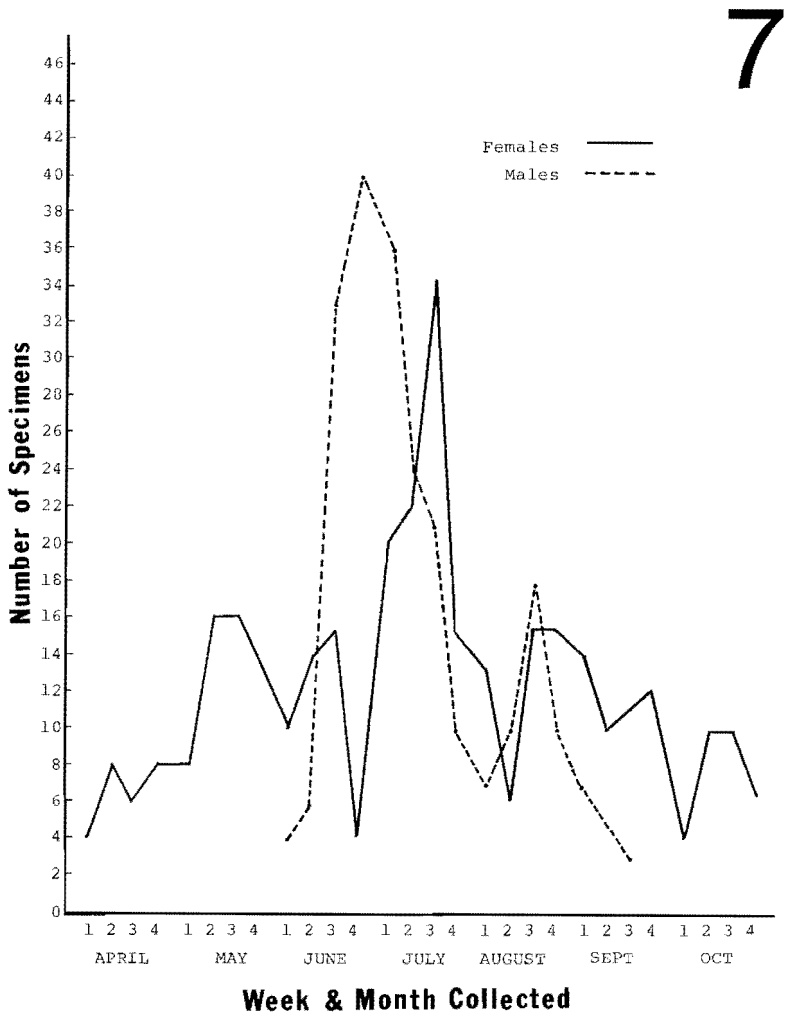


Fig. 7. Collection dates for both sexes of *P. luctuosa*, based upon museum specimens and field observations.

(Fig. 9). Two burrows each contained one female *P. luctuosa* at the bottom, one with two hibernating queen ants (*Acanthomyops* sp.) a few centimeters from the wasp. Another burrow contained two *P. luctuosa* females; one at a depth of 37 cm, the other at the bottom (54 cm). Two immature crickets (*Gryllus* sp.) were found between the wasps at depths of 42 and 46 cm, respectively. Ten females were found at the bottom of another burrow in an enlarged area, 9 cm long. Wasps in the four burrows faced head toward the entrance and were in torpor.

Females found in overwintering burrows were kept in a refrigerator at 5°C until 25 April 1981. The wasps were then transferred to room temperature and released in the field two

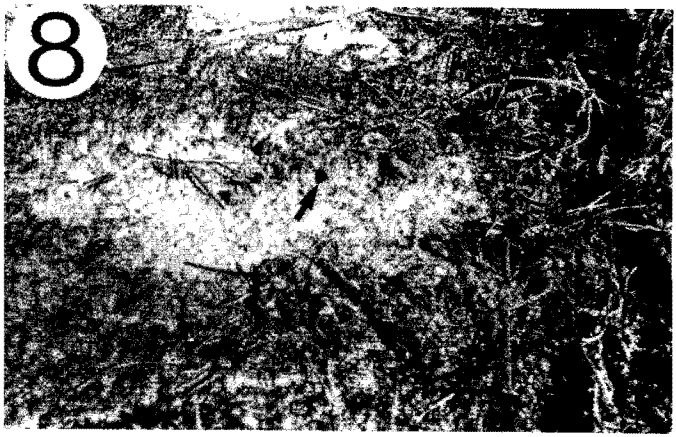


Fig. 8. Entrance of *P. luctuosa* overwintering burrow at Mallory, NY (October 1980).

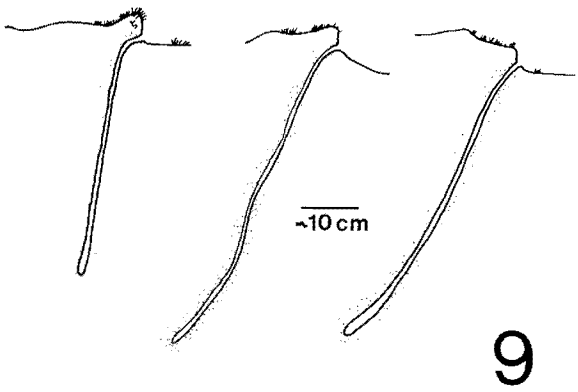


Fig. 9. Side view of *P. luctuosa* overwintering burrows at Mallory, NY.

days later, with no apparent ill effects. While confined in the laboratory in a 20-gallon aquarium with sand, eight females dug shallow resting burrows, with one burrow containing two females.

DISCUSSION

Podalonia closely resembles some Pompilidae in its nesting behavior. Both have the same behavioral formula, as proposed by Iwata (1976) as P-T-I-O-C (P = paralyzation, T = transport, I = nest digging, O = oviposition, C = closure). *Podalonia* caches its prey on plants, as do many pompilids. In comparison with other Sphecoidea, *Podalonia* exhibits "primitive" ethological characters such as the use of a single large prey, simple unicellular nest, mandibular prey transport on ground, and preying on fossorial larvae (Evans 1963b,

1966, Evans and Eberhard 1970, Iwata 1976). The multiple stinging of the prey in *Podalonia* may be a less advanced trait when compared to higher wasps such as *Philanthus* which sting their hymenopterous prey only once in the thorax (Evans 1966). Multiple stinging may coincide with less concentration of locomotory functions in the ganglia of the larval lepidopteran. The stinging pattern observed for *P. luctuosa* is similar to the pattern described for *P. hirsuta* by Bougy (1935) and Gervet and Fulcrand (1970).

In searching for prey *Podalonia* taps its antennae against the substrate, as noted by Bougy (1935) for *P. hirsuta*. Solitary wasps may detect their prey chemically (Iwata 1976) or perhaps with infrared receptors, but neither method has been investigated extensively. *Bonnetia comta* Fallen (Tachinidae) locates burrows of *Agrotis ipsilon* Rottemburg (Noctuidae) by detecting a kairomone in the cutworm's fecal pellets with receptors on its legs and mouthparts (Levin and Clement 1981).

All reports on *Podalonia* nesting behavior have indicated prey cachement on a plant or stick (see Bougy 1935). Such cachement may serve to reduce predatory attacks on the prey, prevent dessication of the cutworm when the sand is hot, or prevent brigandage by conspecifics. Prey cached on plants were not attacked by tiger beetles or ants. Prey left on the ground were invariably attacked by ants or tiger beetles.

The use of pebbles, twigs, fecal pellets, and other debris to fill the upper part of the burrow is not unique to *P. luctuosa*. Bougy (1935), Palmer and Stelfox (1931), Tsuneki (1968), and Bristowe (1971) have reported this behavior for species of *Podalonia* in Europe, Asia, and Australia, respectively. Many species of *Ammophila* also exhibit this behavior (Evans 1959).

Hilarella hilarella is the major parasite of *P. luctuosa*. Newcomer (1930) and Hicks (1932) recorded *H. hilarella* parasitizing *P. luctuosa* in Washington, California, and Colorado. Bougy (1935) found *Hilarella strictica* Meigen parasitizing *P. hirsuta* in Europe. The genus *Hilarella* may be a primary parasite of *Podalonia* throughout its range.

Podalonia has been reported to aggregate during or prior to adverse weather conditions (Roth 1928, Maneval 1939, Hicks 1931a, Grandi 1961, Bohart and Menke 1976). Two of the five overwintering burrows dug at Mallory in November contained more than one wasp. The large number of overwintering burrows at Mallory and the clustering of up to 10 individuals within one burrow suggest that many females dig their own overwintering burrow, with some females sharing burrows, or entering the first one they encounter upon the advent of cold weather. The overwintering and clustering activities of *P. hirsuta* in Europe are similar to those of *P. luctuosa*, but *P. hirsuta* has not been observed to dig overwintering burrows (Roth 1928, Maneval 1939, Grandi 1961).

The presence of two discrete nesting periods and dates of collection support bivoltinism in *P. luctuosa* in New York and probably throughout much of its range. Observations at Mallory revealed three distinct peaks of female activity (Fig. 7): May, when they broke hibernation and nested; July, when the progeny emerged, mated, and nested; and August–September, when females of the next generation mated, fed on nectar, and prepared overwintering burrows. Due to the longevity of a few individuals, some overlap of generations may occur. It is possible that a long-lived male of the first generation could mate with a female of the second generation. Fernald (1927) believed that two generations a year were probable in this species, based upon collection records.

Because *P. luctuosa* nests in the spring and midsummer in a variety of sandy soils and is transcontinental, it may appropriately be termed both an opportunist and generalist in its prey selection. It preys upon at least 20 species of cutworms throughout its range, and probably takes many more. By overwintering, it is able to utilize overwintering larval noctuids early in the spring before they complete development, and, in some areas, avoid parasitism from miltogrammine files which are not present at that time. Wasps nesting in July prey upon different species of cutworms than those in the spring.

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