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ETHOLOGY OF *ANOPLIUS TENEBROSUS* (CRESSON) (HYMENOPTERA: POMPILIDAE)

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Abstract.—*Anoplius tenebrosus* (Cresson) has one generation per year. Females and males emerge in mid-summer in upstate NY. The males die within a few weeks of mating. The females, after mating, feed on flowers, especially goldenrod, and dig overwintering burrows in the ground in late summer and fall. They reappear during the first warm days of spring, and nest in sandy areas bordered by woodlands. Females of *A. tenebrosus* hunt and capture a variety of errant spiders, especially Lycosidae, and store one spider in a shallow, single-celled nest. The prey is cached either on a low plant or on the ground during burrow construction. Transport of the spider to the nest is always backwards on the ground, the wasp usually holding the base of the prey's hind leg with the mandibles. The spider is pulled into the nest by its spinnerets. The wasp's egg is placed obliquely on the venter of the spider's abdomen. *A. viaticus* (L.), a related Palearctic species, has almost identical nesting behavior as *A. tenebrosus*.

Knowledge of the nesting behavior of pompilids is limited, especially in the subgenus *Pompilinus*. There are few particulars for the 17 Nearctic species in this group. Prey preferences of some of the species are narrow, whereas those of others are broad (Evans, 1951). *Anoplius tenebrosus* (Cresson) is one of the commonest pompilids in this subgenus in the Canadian and Transition Zones. The species "occurs in sandy places, particularly in the vicinity of woods; the nest is a short tunnel in the earth with an enlarged terminal cell" (Evans, 1951). Prey spiders comprise Thomisidae and Lycosidae (Evans, 1951; Evans and Yoshimoto, 1962; Wasbauer and Powell, 1962).

Evans (1970) observed *Anoplius tenebrosus* at Jackson Hole, Wyoming from July 4 to August 26. He indicated that females may overwinter because they appear early in the season and that males and fresh females emerged about July 20 after which mating took place. Records of *A. tenebrosus* occurring in the Northwest Territories and the Yukon, Canada were published by Steiner (1970). Kurczewski and Kurczewski (1973) reported Gnaphosidae as a new prey family, described burrow construction, prey transport, nest structure and dimensions, and indicated that females may overwinter.

Our paper describes the ethology of *A. tenebrosus*. The behavior of this species is compared with that of the related Palearctic *Anoplius viaticus* (L.).

Location of nests.—Natural nesting sites comprised sand bordered by woodlands. Data were collected at three sand pits near Mallory, one near Fulton, and

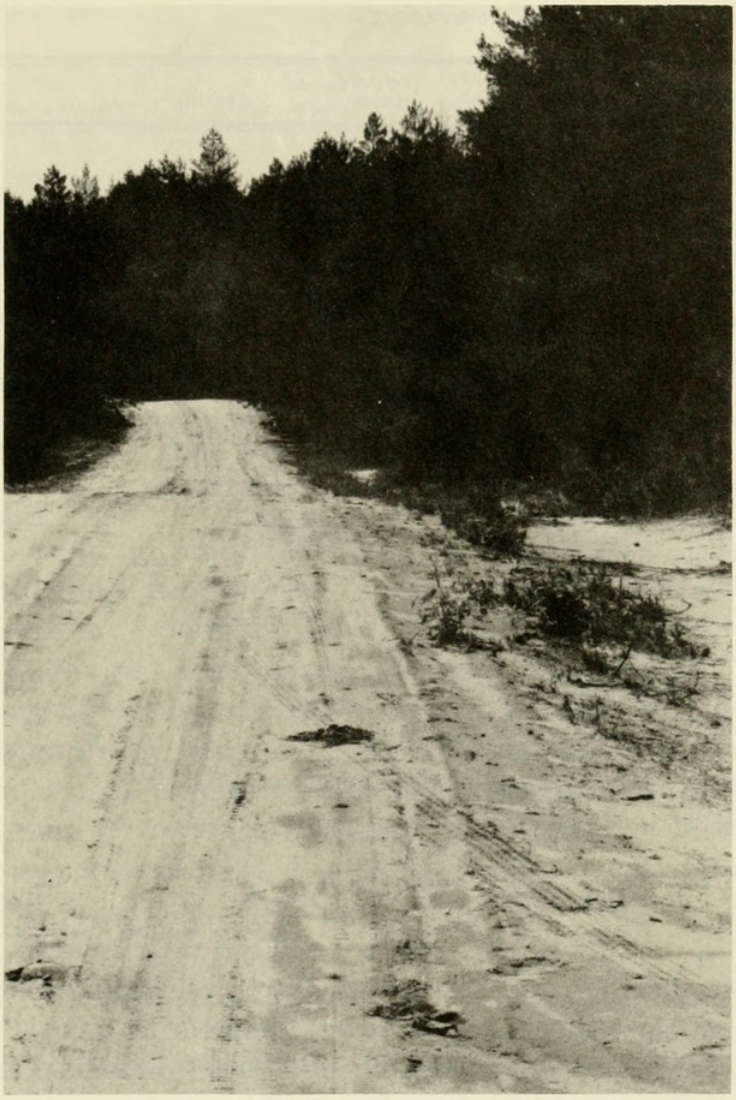

Fig. 1. Sandy road, Boonville, N.Y., in which *Anoplius tenebrosus* nested. (Photograph by R. A. Norton).

one in Selkirk Shores State Park, all in Oswego Co., NY. Other wasps were observed on Camp Road, Boonville. Oneida Co. (Fig. 1), and along a truck trail on the State Campus at Wanakena, St. Lawrence Co., NY.

Females nested in open sand, never under tree canopy. The Mallory, Fulton and Selkirk Shores areas contained sparse mosses, grasses and the remains of the previous years' growth. Deciduous trees and scattered white pine (*Pinus strobus* L.) surrounded these sites; the Wanakena site was bordered by conifers. The soil was moist and firm in the spring when nesting was at its peak (late April or May). Nests were always dug from nearly level ground, even where banks comprised a major component of the sand pit. In 1977 females nested in the central area of a sand pit near Mallory, whereas in 1978 almost all nests occupied a 3 × 8 m area on the northern periphery of the pit.

Associated species.—Early in the spring the bees *Sphecodes persimilis* Lovell and Cockerell, *S. confertus* Say (Halictidae), *Andrena milwaukeensis* Viereck (Andrenidae) and *Colletes inaequalis* Say (Colletidae) occurred in the same soils as *A. tenebrosus*. The only sphecids found nesting early in the spring were the cricket-hunting *Liris argentata* (P-B) (O'Brien and Kurczewski, 1982a) and a caterpillar

Table 1. Prey records for *Anoplius tenebrosus*.

	Species of spider	No. of records	Locality	Reference
Lycosidae				
	Trochosa terricola Thorell imm., ♀	21	Mallory, Boonville, NY	
	Trochosa avara Keys. imm., ♀	16	Mallory, Boonville, NY; Mich	Evans & Yoshimoto, 1962
	Tarentula kochi Keys. ♀	1	Calif.	Wasbauer & Powell, 1962
	Lycosa frondicola Em. ♂	4	Mallory, Boonville, NY; Mich	Evans & Yoshimoto, 1962
	Lycosa gulosa Walck. ♀	1	Boonville, NY	
	Lycosa baltimoriana (Keys.) imm.	1	Mich.	Evans, 1970
	Pardosa moesta Banks ♀	1	Mallory, NY	
	Schizocosa crassipalpata Roewer ♂	1	Mallory, NY	
	Schizocosa saltatrix Hentz	1	NJ	Evans, 1951
			NY	Kurczewski & Kurczewski, 1973
	Schizocosa avida (Walck.)	1		
	Schizocosa sp. (probably *avida*)	1	Boonville, NY	
Thomisidae				
	Xysticus gulosus Keys.	1	Wash.	Evans, 1951
	Xysticus ferox (Hentz) imm., ♀ & ♂	5	Mallory, Fulton, NY; Mich.	Evans & Yoshimoto, 1962
	Xysticus ampullatus Turnbull et al. ♀	1	Selkirk Shores St. Park, NY	
	Xysticus elegans Keys. ♀	3	Mallory, Boonville, NY	
	Xysticus sp. imm.	1	Boonville, NY	
	Thanatus formicinus (Oliv.) ♀	2	MA; NY	Evans, 1970; Kurczewski & Kurczewski, 1973
	Misumena vatia (Clerck) ♀	1	Wanakena, NY	
	Ozyptila distans Dondale & Redner ♀	1	Wanakena, NY	
Agelenidae				
	Wadotes hybridus Em. ♀	2	Boonville, NY	
	Wadotes sp. imm.	1	Boonville, NY	
	Tegenaria domestica (Clerck) imm. ♂	1	Boonville, NY	
Gnaphosidae				
	Haplodrassus signifer (Koch) ♀	1	NY	Kurczewski & Kurczewski, 1973
	Zelotes subterraneous (Koch) ♂	1	Wanakena, NY	
	Drassulus sp. ♂	1	Wanakena, NY	
Salticidae				
	Pellenes sp. imm.	1	Boonville, NY	

Table 1. Continued

Species of spider	No. of records	Locality	Reference
Amaurobiidae			
Callobius bennetti (Blackwall) ♀	1	Wanakena, NY	
Clubionidae			
Agroeca ornata Banks ♀	1	Boonville, NY	

hunter, *Podalonia luctuosa* (Smith) (O'Brien and Kurczewski, 1982b). Another pompilid that nested at this time was *Priocnemis* (*Priocnemissus*) *minorata* Banks. *P. minorata* nested in the wooded edges of the sandy roads near Boonville, NY.

Parasites.—At Boonville, a female of *Metopia argyrocephala* (Mg.) (Sarcophagidae: Miltogramminae) entered a nest of *Anoplius tenebrosus* when the wasp was out retrieving her prey. Upon excavation of the nest, the wasp's egg was found to be destroyed and a small maggot was located on the spider. The maggot, which was reared to an adult *M. argyrocephala,* had been deposited before the prey or egg of *A. tenebrosus* had been placed in the nest. Another nest contained three unidentified maggots on a spider, and the egg of *A. tenebrosus* had been destroyed.

Predators.—*Anoplius tenebrosus* females were attacked unsuccessfully by the cicindelids *Cicindela scutellaris lecontei* Haldeman, *C. repanda* Dejean, and *C. formosa generosa* Dejean. However, the beetles fed upon the spiders captured by *A. tenebrosus.* One cicindelid punctured the spider's abdomen which caused the wasp to release the prey and attack the beetle. The wasp was successful in driving off the beetle but the damaged prey was unsuitable for provisioning and was abandoned after the female fed on its body fluids. This wasp was then "offered" another, paralyzed spider which had been abandoned by a female. It was readily accepted and used for provisioning.

Prey.—*A. tenebrosus* preys on at least 25 species of spiders belonging to seven families. The majority are errant spiders, but some are funnel-web spinners (Agelenidae) or those which spin loose, irregular webs (Amaurobiidae). The prey consist primarily of Lycosidae of which *Trochosa terricola* Thorell is the predominant species (Table 1).

The average weight of a paralyzed prey was 92.39 mg (16.1–210.2, $n = 91$), while that of a recently killed wasp was 40.16 mg (11.0–72.0, $n = 48$). An average prey to wasp ratio in this species approximated 2.3 to 1 which coincides with other pompilid prey to wasp ratios (Iwata 1942). Since only one prey was stored for the larva, it must be of sufficient size to permit larval development. One larva did not complete development on a small spider (16.1 mg).

Activity conditions.—Nesting began the last week of April and ended during the second week of June in upstate New York. Little or no activity was observed on cold, cloudy days, during periods of drought or high temperatures. One female was observed digging as it began to rain. The temperature had dropped to 17°C, she was moving slowly and managed to bring her prey into the nest, but never

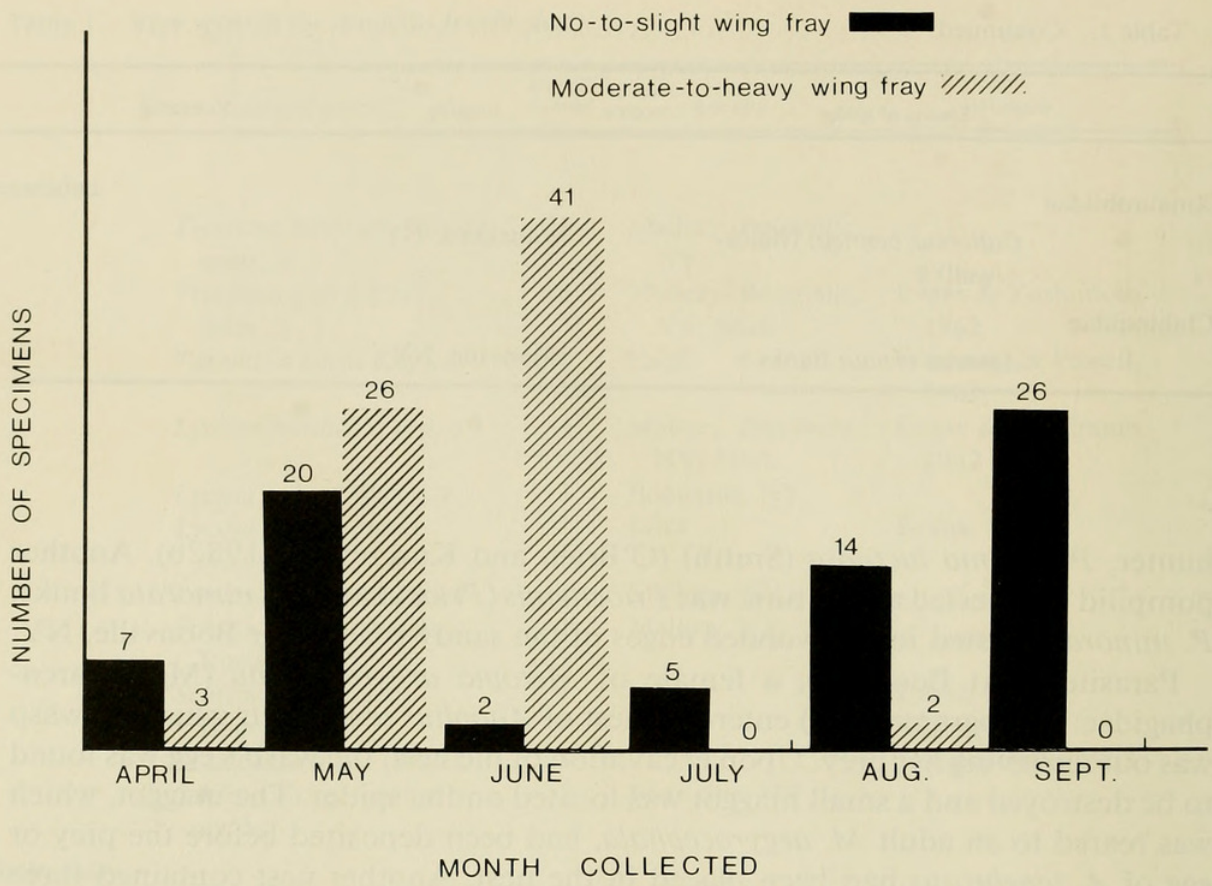

Fig. 2. Number of ♀ *Anoplius tenebrosus* with no-to-slight and moderate-to-heavy wing fray in relation to the month of collection.

came out. The nest was still open the next day and, upon excavating it, we found the female in a small cell off the main tunnel above the provisioning cell.

Females nested continuously throughout the day from when the ambient temperature exceeded 15°C up to 32°C or until the temperature dropped below 16°C late in the afternoon or at twilight. Females then either dug shallow overnight burrows in the sand or burrowed into moss and spent the night. Some wasps used what appeared to be abandoned tiger beetle or bee tunnels, but usually examined several holes before settling on a site.

No hunting or nesting occurred in the fall; rather, females spent much time feeding on goldenrod, *Solidago* spp. They walked to the blossoms if the temperature was low (ca. 17°C) or flew if the temperature was higher. This activity continued until the goldenrod had finished blooming in October.

Overwintering.—In the fall of 1977 seven females were marked with vital paint at Mallory, NY. One female was recaptured in the spring, proving that some wasps overwinter. On October 5, 1978 one female was dug out of a burrow, 21 cm deep. She had entered the burrow on October 3rd and may have overwintered there.

Circumstantial evidence supports a univoltine existence and overwintering of females. Based upon wing condition, there were two appearances of the females (Fig. 2). Field studies demonstrated that wasps found during late summer and early fall were mating, feeding on nectar, and building overwintering burrows, whereas those observed during spring were nesting. Males were present only in summer (July–September).

Activity of males.—Males of *Anoplius tenebrosus* flew erratically above the sand, searching for females. They were collected on the flowers of *Daucus carota* L.

Prey capture.—Hunting took place in the spring in the fields or woodlots surrounding the nesting area. Females ran on and through vegetation and periodically made short flights. They flicked their wings continuously and tapped their antennae constantly on the substrate.

Two females were observed fighting over a small gnaphosid, lapping up body fluids from a hole in its abdomen. This spider, not used for nesting, was abandoned by both wasps. Another female was seen sucking body fluids from a spider's cephalothorax, after stinging it.

Females were observed moving excitedly through clumps of grass which harbored spiders. Wasps captured errant spiders by pouncing on their dorsum and curving the abdomen underneath in order to insert the sting in the cephalothorax.

At Mallory *A. tenebrosus* almost invariably placed the spider in a clump of grass, moss or dried fern before digging the nest. At Boonville approximately half of the females left their prey on the sand. Some wasps moved their prey closer to the nest after burrow construction had begun and they examined it several times during the construction. If the prey had fallen from its cachement the wasp repositioned it before returning to her nest.

Nesting behavior.—Females dug burrows at angles of approximately 70–90° to the sand surface (Fig. 3). Each burrow ended in an enlarged, terminal cell. The average entrance diameter was 5.6 mm (5–7, $n = 15$). The mean distance from the soil surface to the bottom of the cell was 3.8 cm (1.8–6.8, $n = 45$). The cell averaged 9.1 (6–13, $n = 47$) × 7.5 mm (5.5–10, $n = 35$).

Digging was initiated in depressions in the sand, frequently hoof- or footprints. Some females dug down a few millimeters but abandoned these excavations and dug elsewhere. Females began digging by spreading the legs and biting the sand with the mandibles. The mandibles loosened the sand while the forelegs alternately swept it back under the abdomen. The mesothoracic legs were used to pass loads of sand from the forelegs to the hindlegs which would then push the sand up the burrow. When several loads had been deposited behind the wasp, she would back up the burrow while pushing the sand into the entrance with the hindlegs. At the entrance the female would back out, using the meso- and metathoracic legs, while the forelegs swept the sand back under the abdomen. After several such backings, a low, fan-shaped tumulus extended approximately 6 cm from the entrance.

One female started to dig, abandoned the burrow and started another within a few centimeters of the first. She continually confused the two locations and, after checking on her prey, returned to one nest one time and the other the next. This continued until both nests were nearly completed and culminated with the completion and provisioning of one nest.

The female coming out of the nest head first signified the completion of the burrow and cell. The entrance was left open as the wasp retrieved her spider. Females averaged 36 (16–70, $n = 14$) minutes to dig a nest, the time varying with soil texture, moisture content, wasp's age, ambient temperature, and size of prey. The maximum duration was for a female digging in dry, hard-packed sand.

Prey transport and provisioning.—Prey transport involved pulling the spider backwards, usually by the base of a hind or other leg, with the mandibles. A few wasps grasped prey by a foreleg and held the spider upside down while walking

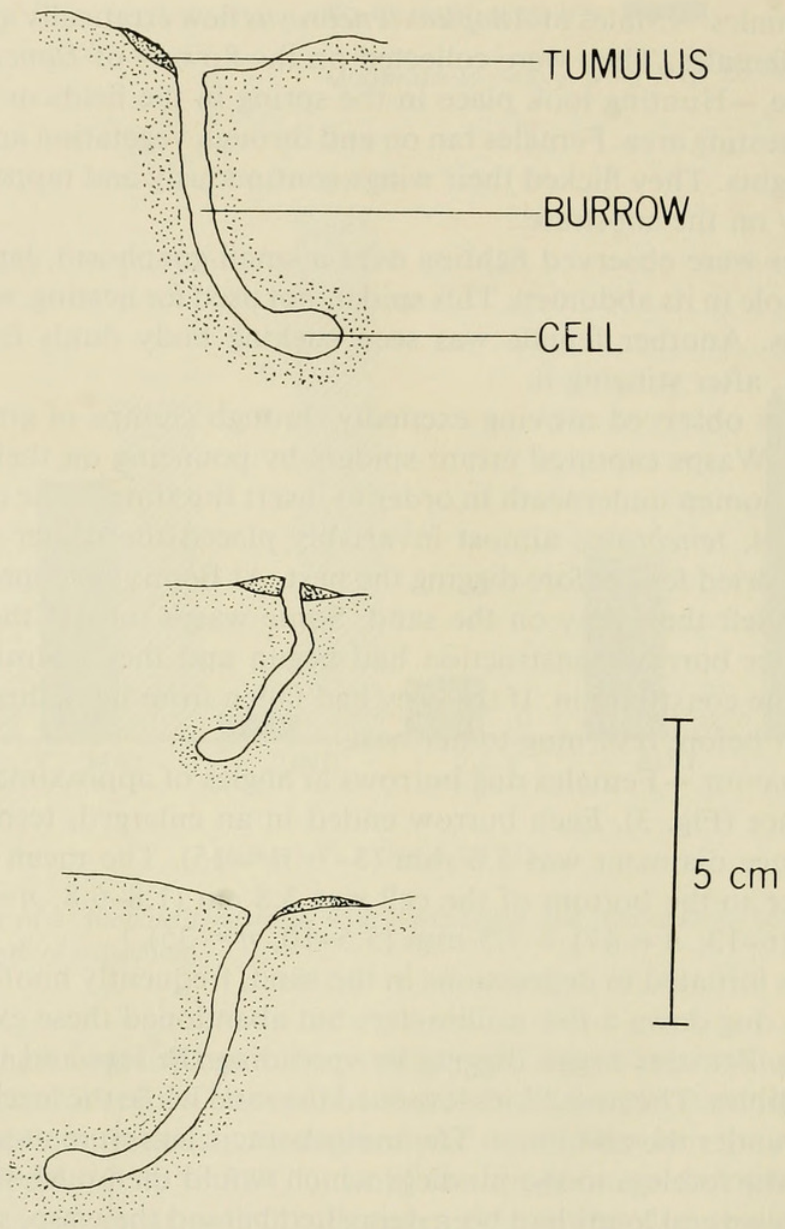

Fig. 3. Side views of nests of *Anoplius tenebrosus*, showing burrows, terminal cells and tumuli.

backwards. During transport, a female usually dropped her spider before reaching the entrance. If the spider had been cached some distance from the nest, females released their prey several times and reoriented. After a wasp had dropped her prey near the entrance, she grasped it by the base of a hind coxa, a pedipalp, or the distal part of a leg and positioned it, dorsum up, spinnerets toward the entrance. Females then entered head first, turned around inside and came out head first. They grasped the spider by the spinnerets with the mandibles and pulled it into the nest, except in one case when a large thomisid was pulled in by the base of a hind leg. The spider was often positioned in the cell dorsum upward and head outward. The legs formed a plug at the proximal end of the cell for the sand closure.

Closure.—Closure of the nest began after the egg had been laid, based upon wasps observed between glass partitions. The female broke in the sides of the burrow with the mandibles and tamped the sand with the tip of the abdomen as

Fig. 4. *Trochosa terricola* with egg of *Anoplius tenebrosus* on venter of abdomen. (Photograph by R. A. Norton).

she moved up the burrow. When she neared the entrance she used the forelegs alternately to scrape in the loose sand on the surface that had been removed during digging. The tip of the abdomen packed the sand in the burrow and smoothed it flush with the surrounding sand. The female then alternately swept sand under her body with the forelegs in the direction of the filled entrance. Some females placed small pebbles, grass, or twigs on the filled entrance. The wasp then usually cleaned herself and flew off.

Eclosion, larval and pupal development.—Seven eggs averaged 2.4 × 1.0 mm in size and were placed rather obliquely on the venter of the spider's abdomen (Fig. 4). Variability in egg placement was due to variation in the size and species of prey. In the laboratory, 23 eggs from Mallory and Boonville eclosed in 2–3 days at ambient temperatures of 21°–26°C. Larval and pupal development lasted 31 days for one male; 35, 46 and 64 days for three females.

Discussion

Anoplius tenebrosus is nearly identical to the Palearctic *A. viaticus* in its nesting behavior (Table 2). Both species mate during the summer after which the males die. The females of both *A. tenebrosus* and *A. viaticus* do not hunt during the late summer or fall but feed on nectar, overwinter in relatively deep burrows, reemerge in the spring and provision short, shallow nests with paralyzed wandering spiders.

Females of *A. viaticus* dig overwintering burrows, 15–30 cm deep (Adlerz, 1903; Schütze, 1921–24; Nielsen, 1932; Grandi, 1961; Wolf, 1971). But Soyer (1963), working in France, found overwintering burrows of this species to be only 5–6 cm deep—perhaps a reflection of a shallower substrate freeze line at this latitude. We found one female of *A. tenebrosus* overwintering in a burrow, 21 cm deep. Schütze (1921–1924) found as many as 50 overwintering burrows of *A. viaticus*

Table 2. Ethological comparison of *Anoplius tenebrosus* and *A. viaticus*.

Anoplius (*Pompilinus*) *tenebrosus* (Cresson)	*Anoplius* (*Pompilinus*) *viaticus* (Linnaeus)
Overwintering stage: adult	Overwintering stage: adult
Generations per year: one	Generations per year: one
Depth of overwintering burrow: 21 cm	Depth of overwintering burrow: 15 cm (Schütze, 1921–24); 15–20 cm (Nielsen, 1932); 30 cm (Adlerz, 1903); 5–6 cm (Soyer, 1963)
Cell depth (surface to bottom): $\bar{x}$ = 3.8 cm (range 1.8–6.8)	Cell depth (surface to bottom): (2–6 cm)
Cell length: $\bar{x}$= 9.1 mm (range 6–13)	Cell length: 12 mm
Prey cache: in plant or on ground	Prey cache: in plant or on ground
Prey transportation: backwards by the base of a hind leg; pulled into nest by spinnerets	Prey transportation: backwards by the base of a hind leg; pulled into nest by spinnerets
Egg placement: obliquely on the abdomen	Egg placement: obliquely on the abdomen
Nest closure: first by breaking in the sides of the burrow, then sweeping in sand with the forelegs, which is pressed down with the tip of the abdomen	Nest closure: first by breaking in the sides of the burrow, then sweeping in sand with the forelegs, which is pressed down with the tip of the abdomen
Prey: primarily Lycosidae	Prey: primarily Lycosidae
Ethological type: VPTIOC	Ethological type: VPTIOC

in a single area. Wolf (1971) noted that overwintering burrows of this species always faced southward as did those of *A. tenebrosus*.

Four other European pompilids, *Priocnemis perturbator* (Harris), *P. coriacea* (Dahlbom), *P. propinqua* (Lepeletier) and *Dipogon intermedius* (Dahlbom) overwinter as adult females, according to Richards and Hamm (1939). Additional Nearctic species of Pompilidae with northern ranges of distribution may also overwinter as adults but it remains to mark and recapture the females in order to ascertain this. One explanation of female overwintering and spring provisioning in *A. tenebrosus* may involve lessening egg and larval predation by miltogrammine flies (Sarcophagidae) and other summer cleptoparasites.

Burrow construction and final closing behavior are similar in *A. tenebrosus* and *A. viaticus*. Soyer (1963) found females of the latter taking 15–65 ($\bar{x}$, 28) min. to construct a burrow, and we recorded females of *A. tenebrosus* taking 16–70 ($\bar{x}$, 36) min. for this behavior. The nests of the two species are equivalent in form and dimensions (see Soyer, 1963; Bonelli, 1966; Wolf, 1971; for *A. viaticus*). Ferton (1897) noted a female of *A. viaticus* that constructed more than one cell from a single burrow. Bonelli (1966) reported that several burrows of *A. viaticus* were built and visited before each was stored with a spider. Both of these observations need confirmation.

The prey species found in the nests of the two species of *Anoplius* are similar, with a preponderance of one lycosid, *Trochosa terricola*. Five families of prey are identical, emphasizing the selection of wandering spiders of similar ecological

requirements and suggesting similar hunting behaviors for the two species of wasps (see Picard, 1903; Adlerz, 1903; Bristowe, 1928; for *A. viaticus*).

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