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Frank E. Kurczewski
S.U.N.Y. College of Environmental Science and Forestry

Edmund J. Kurczewski

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NEST AND PREY OF *AGENIELLA (LEUCOPHRUS) FULGIFRONS* (HYMENOPTERA: POMPILIDAE)

Frank E. Kurczewski[1] and Edmund J. Kurczewski[2]

ABSTRACT

Information on the habitat, nest-site, hunting, prey transport, closure, burrow structure, and prey of *Ageniella (Leucophrus) fulgifrons* is presented. Components of the nesting behaviors of other species of *Ageniella* are examined and compared with those of *A. fulgifrons*.

Little is known about the nesting behaviors of the Nearctic species of *Ageniella* (Evans and Yoshimoto 1962). Prey records have been published for several of the species (Krombein 1979), but the first nests of Nearctic members of this genus were described only rather recently (*A. blaisdelli* (Fox) [Wasbauer and Leech 1973]; *A. conflicta* Banks [Evans 1974]). Janvier (1930) has presented rather detailed observations on the nesting of a Neotropical species, *A. argenteosignata* Spinola.

A. (Leucophrus) fulgifrons (Cresson) is a medium-sized, all-black spider wasp with golden reflective vestiture on the clypeus, frons, and face. It occurs in the Upper and Lower Austral Zones from the Atlantic Ocean to 100°W long. (Krombein 1979). The species is found in fields and meadows and preys upon Salticidae (Evans 1959, Kurczewski and Kurczewski 1968). It is collected in the same habitat as the pompilid *Entypus unifasciatus* (Say) and the sphecids *Ammophila urnaria* Dahlbom and *Cerceris clypeata* Dahlbom. Like these other species, *A. fulgifrons* visits the flowers of *Daucus carota* L. for nectar (Kurczewski 1961a).

On 17 July 1985 at 1310 h (EDT) at the edge of an overgrown field bordering an abandoned gravel pit, 2.4 km SE of Erie, Erie County, PA, a female of *A. fulgifrons* was observed transporting a salticid which had all legs amputated at the coxal-trochanteral joints. The provisioning wasp walked forward out of the field for ca. 1 m and then paused atop her prey for 25 sec. She repositioned her paralyzed spider, grasped it by its spinnerets with the mandibles, and, straddling it, proceeded forward on gravelly soil for 45 cm directly into a mole burrow.

After waiting for 40 min we excavated the 25-mm-wide tunnel. The soil contained much clay and many large stones. The mole burrow bifurcated 5 cm beneath the surface with one tunnel coursing horizontally and the other plunging downward at a 60° angle to the surface for 21 cm and then ending blindly (Fig. 1). At a depth of 18 cm we unearthed a cell, 6 × 13.5 mm in size, containing a paralyzed *Phidippus audax* (Hentz) female (Salticidae). All of the spider's legs had been amputated as described above. The cell was positioned obliquely-vertically in the soil with the spider's cephalothorax uppermost. We could not find the wasp's egg on the spider's abdomen. The spider weighed (wet) 90 mg.

We collected the female of *A. fulgifrons* at a depth of 18.5 cm, 3 cm from the first cell, in a small side burrow, 4.5 mm in diameter (Fig. 1). She was in a head-upward position,

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[1]Department of Environmental and Forest Biology, S.U.N.Y. College of Environmental Science and Forestry, Syracuse, NY 13210.

[2]2921 Reed Street, Erie, PA 16504.

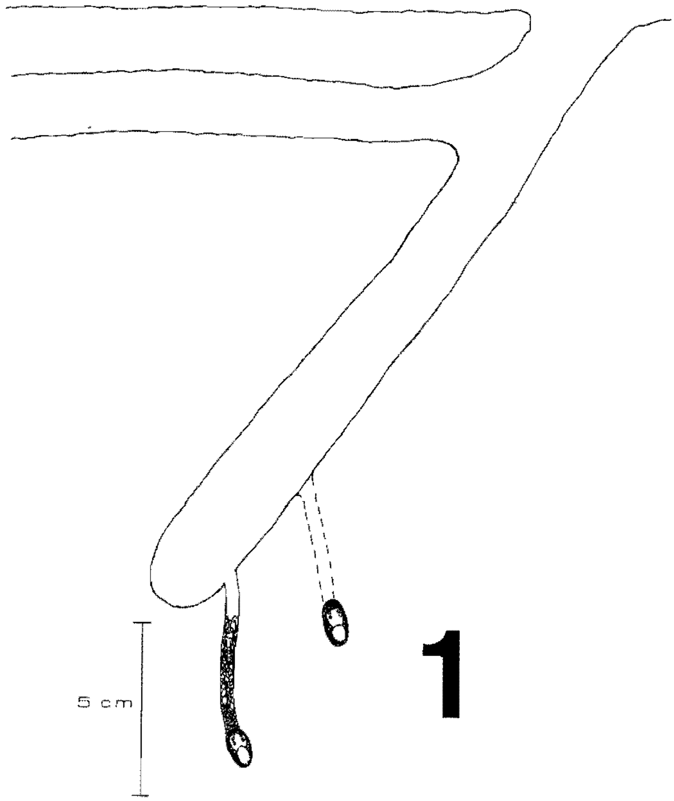

Fig. 1. Two burrows of *Ageniella (Leucophrus) fulgifrons*, as viewed from side, showing cells, paralyzed spiders, and wasp filling in lower burrow. Scale to left refers to both nests and mole tunnel.

pulling gravel particles into the tunnel with the mandibles and forelegs (?). The burrow, open for 2.5 cm at the top, descended almost vertically for an additional 2 cm, was filled with pebbles and soil, and ended in a cell, 6 × 11.5 mm. The cell contained a paralyzed *Eris* sp., probably *marginata* (Walckenaer), immature female (Salticidae) positioned cephalothorax upward, with all legs amputated. This prey was observed being transported on the ground surface. The wasp's egg could not be found and may have been dislodged from the spider's abdomen during the excavation. The spider weighed (wet) 72 mg and the wasp, 48 mg.

On 27 July 1985 at 1535 h at the opposite side of the gravel pit, another female of *A. fulgifrons* was seen to enter a mole tunnel, ca. 25 mm wide. This burrow was located in a sandy-gravelly slope of a car path leading into the pit. The wasp exited at 1546 h, circled the entrance three times, walking in a ''stilted'' fashion, flew 2 m away, paused, and then flew into an overgrown field. After 45 min the female had not returned to the site.

On 24 July 1986 at 1210 h, a female was observed hunting through low vegetation, primarily *Solidago* spp., grasses, *Fragaria* sp., and *Trifolium* sp., in the overgrown portion of the gravel pit. She continually moved her antennae as she walked rather slowly up and down the stems and on the leaves of the plants. Occasionally, she paused and cleaned the antennae. Her wings were held mostly flat on the dorsum and only occasionally bobbed up and down. She made no flight from one area to another, while hunting, but proceeded walking and searching in a seemingly random manner.

A female was seen on 28 July 1986 at 1330 h, filling a burrow in a depression at the edge of a field with twigs, dried grass blades, and pebbles. She held the wings flat on the dorsum as she walked backwards carrying debris with the mandibles. Each time she turned 180° to place the debris on the fill and, after several such trips and a small mound of debris had accumulated, she flew away. We were unable to trace the burrow due to several subterranean rocks.

DISCUSSION

Like many other species of Pompilidae, species of *Ageniella* are habitat-specific. In the eastern United States *A. (Ageniella) accepta* (Cresson), *A. (Ageniella) conflicta* and *A. (Leucophrus) semitincta* (Banks) are predominantly psammophilous, *A. (Ageniella) norata* Banks and *A. (Ageniella) cupida* (Cresson) are silvicolous, and *A. (Leucophrus) fulgifrons* inhabits fields and meadows (Townes 1957; Kurczewski 1961b; Evans and Yoshimoto 1962; Kurczewski and Kurczewski 1963, 1968; Evans 1974).

Evans and Yoshimoto (1962) have reported *A. (Priophanes) arcuata* (Banks) nesting in Kansas in a "previously prepared" burrow in sand which appeared to have been dug by the wasp. In the subgenus *Priophanes* prominent teeth on the hindtibiae may assist in pushing soil upward in the burrow (Evans and Yoshimoto 1962). The legs of members of the subgenus *Ageniella*, on the other hand, are smooth and devoid of spines and these species probably do not use the legs for soil removal. The Nearctic species of *Ageniella s. str.* apparently build short nests in the soil from pre-existing burrows or cavities. For example, Hartman (1905) noted either *A. accepta* or *A. conflicta* (reported as *A. accepta*) nesting in Texas in a vertical burrow "three inches deep" from the bottom of a crevice, "two inches deep." Wasbauer and Leech (1973) reported *A. (Ageniella) blaisdelli* nesting from the side of an active burrow of *Astata occidentalis* Cresson in California. Evans (1974) found both *A. conflicta* and *A. (Ageniella) partita* Banks transporting paralyzed spiders into inactive *Philanthus gibbosus* (Fabricius) burrows in Massachusetts. Our observations on *A. fulgifrons* nesting within mole tunnels extend the use of pre-existing cavities to the subgenus *Leucophrus*. Townes (1957) noted females of *A. (L.) semitincta* exploring drying cracks in a bare red-clay bank. One wasp had the top of her head and thorax "plastered" with dried red mud. Females of *Leucophrus* lack a pygidium and have only weak longitudinal teeth on the hindtibiae (Townes 1957).

The Neotropical *A. argenteosignata* is an enigma. Townes (1957) assigned this species to the subgenus *Ageniella* yet Janiver (1930) noted females digging their own nests among the bases of grasses near fissures in the ground and building from 8 to 12 cells per nest, the cells ranging in depth from 2 to 15 cm. The first cell was constructed before hunting began and subsequent cells were built successively deeper from a common burrow. The same pattern of cell succession was evident in the two cells of *A. fulgifrons* that we unearthed near the mole tunnel. The uppermost cell was older than the deeper one as indicated by the amount of moisture on the spider and the fact that we unearthed the wasp as she was filling the burrow to the lower cell.

Evans (1974) noted that completed burrows of *A. conflicta* were filled with "small pebbles, bits of leaves, and grass blades. . . . " Such a closure would be expected in a species which lacks fossorial spines on the legs. The burrow closure of *A. fulgifrons* in one nest we excavated also contained pebbles and soil particles but no vegetable material. However, another female observed a year later filled her burrow with twigs, dried grass blades, and pebbles.

A. fulgifrons resembles *A. semitincta* and another auplopodine pompilid, *Phanagenia bombycina* (Cresson), in hunting for prey on the ground and low vegetation, by occasionally bobbing the wings up and down but not flicking them incessantly, and by rarely flying from one area to another. Species in the pompiline genus *Anoplius*, while hunting, flick the wings continuously and fly rapidly from one site to another (Evans and Yoshimoto 1962).

In *Ageniella* and the related genera *Phanagenia* and *Auplopus* the manner of transport of the prey, i.e., forward on the ground or in short flights while straddling the spider, is facilitated by amputation of the prey's legs at the coxal- trochanteral joints (see Evans and Yoshimoto 1962). Hartman (1905) described a female of either *A. accepta* or *A. conflicta* that amputated one of the prey's legs, then straddled the spider and tried to walk forward. The spider's other legs interfered with this manner of transport so the wasp released it, amputated two more legs, attempted to transport the prey, released it again and cut off all of the spider's legs before moving it.

Janvier (1930) observed that *A. argenteosignata* amputated the prey's legs during transport prior to nest entry. The wasp snipped off the spider's posterior legs with the mandibles at the coxal-trochanteral joints and then moved forward as it cut off the anterior legs. Many stored prey had all of the legs amputated but some had one, two, or three legs intact (see Fig. 2, Janvier 1930).

In some reports on species of *Ageniella*, where all of the legs had been amputated, the spider was grasped by its anterior end, probably dorsal side up, and carried forward either on the ground or in short flights (*A. argenteosignata* [Janvier 1930]; *A. conflicta* [Evans and Yoshimoto 1962, Kurczewski and Kurczewski 1968]; *A. partita* [Evans and Yoshimoto 1962]; *A. arcuata* [Evans and Yoshimoto 1962]; *A. (Priophanes) agenioides* (Fox) [Kurczewski and Kurczewski 1968]). Evans (1964) ascertained that in *A. (Ageniella) nivalis* (Cameron) the wasp grasped the base of the right chelicera of the spider while moving forward. Kurczewski (1963) noted a female of *A. partita* maintaining an anterior grasp of the prey during forward transport but this spider had all of its legs intact.

Other observations of prey transport in this genus reveal different grasps of the prey's body. Evans and Yoshimoto (1962) reported a female of *A. conflicta* that ran forward while grasping the end of one of the spider's legs. None of the spider's legs had been amputated. Evans (1974) noted a female of *A. partita* running on the ground and making short flights while straddling the prey and holding it by the spinnerets, a grasp that we confirmed in *A. fulgifrons*. In *A. partita* only one leg had been amputated but in *A. fulgifrons* all of the spider's legs had been cut off. A provisioning wasp may alter her grasp of the spider during transport depending upon the number of legs amputated, size and shape of the prey, and proximity of the pair to the nest. We observed that *A. fulgifrons* paused atop the spider and readjusted it prior to transporting it into the mole tunnel while grasping the prey by its spinnerets. Such a grasp may have facilitated transport into the nest, as was the case in *A. argenteosignata* (Janvier 1930) and, possibly, *A. partita* (Evans 1974).

Strangely, none of the spiders unearthed from any cell in studies on the Nearctic species of *Ageniella* contained an egg on the abdomen. The cell of *A. accepta* or *A. conflicta* that Hartman (1905) excavated had not been provisioned. That of *A. arcuata* unearthed by Evans and Yoshimoto (1962) contained a spider but the egg "had not yet been laid." The cell of *A. blaisdelli* dug by Washbauer and Leech (1973) likewise contained a spider but no wasp egg. Evans (1974) did not report finding eggs on the prey of *A. conflicta* or *A. partita*, nor did we find any eggs associated with the stored prey of *A. fulgifrons*. Either the egg is lightly affixed to the spider's abdomen and is brushed off during the prey's removal from the confines of the cell (as frequently occurs in species of *Episyron*) or it had not yet been laid by the provisioning wasp due to some unexplained ovipositional delay (as seemed to be the case in some of the above-mentioned observations). The egg of *A. argenteosignata* is laid in an oblique position about midway on the spider's abdomen (see Fig. 1, Janvier 1930) and the larva begins feeding at this point of attachment.

In 1951 Townes assigned the Nearctic species of *Ageniella* to five subgenera using adult external morphology. Based upon the prey records available for species of *Ageniella* (see Janiver 1930, Krombein 1979), there is no specificity for a family of spider at the subgenus level (Table 1). In *Leucophrus*, *A. fulgifrons* attacks Salticidae while *A. semitincta* preys upon Agelenidae. *A. (Nemagenia) longula* (Cresson) captures Lycosidae (three records) and *A. (Ameragenia) salti* (Banks) takes Clubionidae (two records), but

Table 1. Families of prey of subgenera and species of *Ageniella*.

Ageniella	Prey family						
	Agelenidae	Lycosidae	Oxyopidae	Gnaphosidae	Clubionidae	Thomisidae	Salticidae
Leucophrus							
fulgifrons							X
semitincta	X						
Nemagenia							
longula		X					
Priophanes							
agenioides						X	X
arcuata			X			X	X
faceta		X					
fuscipennis			X			X	
Ageniella							
accepta		X					
argenteosignata				X			
blaisdelli		X					
conflicta		X					
coronata					X		
euphorbiae	X	X					
evansi		X					
nivalis		X					
partita		X		X			
vogeli		X					
Ameragenia							
salti					X		

there are no records available for other species in these subgenera to substantiate such preferences. Four species in the subgenus *Priophanes* prey upon a total of four families of spider, with three of them each capturing two or more families. Only in the subgenus *Ageniella* where eight species prey upon Lycosidae, one, Gnaphosidae, and one, Clubionidae, is there a semblance of selectivity. But two of the eight species that hunt Lycosidae also capture Agelenidae and Gnaphosidae, respectively.

Although some pieces of the puzzle have been put together regarding the intricacies of the nesting behaviors of species of *Ageniella*, much has yet to be learned before a behavioral synopsis can be attempted. Habitat preferences for additional species have to be ascertained along with whether or not particular species construct their own nests or use pre-existing cavities. The specific method of prey transport of various species must be detailed and correlated with leg amputation, size, shape and kind of prey, and entry into the nest. The exact position of the affixation of the wasp's egg on the spider must be determined and compared with that of *A. argenteosignata* and species of *Phanagenia* and *Auplopus*. Finally, much has yet to be learned about prey specificity in the various species of *Ageniella* in order to delimit subgenera and species groups.

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