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Aposematic-habitat correlation in Nearctic species of *Episyron* Schiødte (Hymenoptera: Pompilidae: Pompilinae: Pompilini)

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Abstract. Three Nearctic species of *Episyron* Schiødte (Hymenoptera: Pompilidae: Pompilinae: Pompilini) were examined morphologically, geographically, and ecologically with intent to infer an aposematic correlation with habitat type, protarsal digging rake morphology, and host spider association. *Episyron quinquenotatus quinquenotatus* (Say) and *E. conterminus cressoni* (Dewitz), two subspecies with extensive aposematic markings and more and longer protarsal comb spines, were associated with bare or sparsely vegetated sandy soils near water courses. *Episyron biguttatus biguttatus* (Fabricus), with few aposematic markings and less and shorter protarsal comb spines, was associated with more densely vegetated terrain and gravelly and loamy soils. Three subspecies of *Anoplius apiculatus* (Smith) (Hymenoptera: Pompilidae: Pompilinae: Pompilini) are discussed as an aposematic-habitat comparison.

Key words. *Episyron quinquenotatus quinquenotatus, Episyron conterminus cressoni, Episyron biguttatus biguttatus*, aposematic body coloration, habitat type, protarsal digging rake morphology, host spider association, *Anoplius apiculatus*.

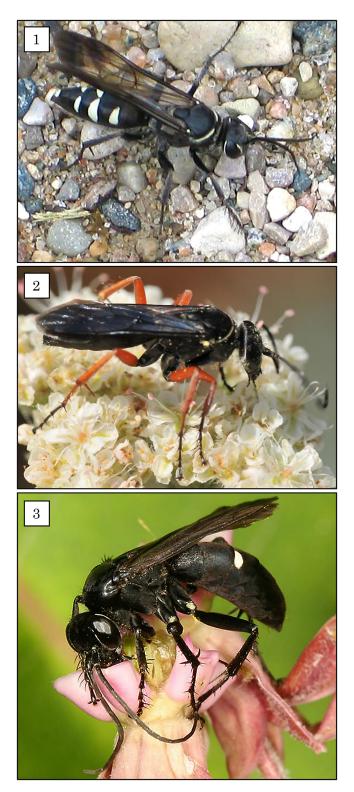
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Introduction

Bright and contrasting aposematic coloration (red, orange, yellow, or white on a black body) in spider wasps (Hymenoptera: Pompilidae) is often associated with open terrain and sparse or no vegetation. Three Nearctic subspecies of *Episyron* Schiødte, *E. quinquenotatus quinquenotatus* (Say) (Fig. 1), *E. conterminus cressoni* (Dewitz) (Fig. 2), and *E. biguttatus biguttatus* (Fabricius) (Fig. 3) were examined to test this hypothesis. The three subspecies are comparable in size, the females averaging 10–12.5 mm in body length (Evans 1950). East of the Rocky Mountains, *Episyron b. biguttatus* and *E. q. quinquenotatus* females are black with whitish markings on the inner and outer eye orbits, posterior pronotal margin, behind the tegulae, and metasomal tergites (Evans 1950). *Episyron b. biguttatus* usually has only a pair of whitish spots on metasomal tergite 3 and may lack whitish marking on the posterior pronotal margin. *Episyron q. quinquenotatus* has a whitish spot on the apical metasomal tergite and paired whitish spots or single united whitish bands on tergites 2, 3, and 4. On the West Coast, females of different subspecies are basically black [*E. quinquenotatus hurdi* Evans] or bluish black [*E. biguttatus californicus* (Banks)] (Evans 1950; Wasbauer and Kimsey 1985). *Episyron conterminus cressoni* (Dewitz) females have pale yellowish markings on the inner and outer orbits, neck, posterior pronotal margin, behind the tegulae, and, sometimes, paired spots on metasomal tergite 3 (Evans 1950, 1966). Tibiae and femora of *E. conterminus cressoni* are rufous.

Episyron q. quinquenotatus occurs from Canada to the Gulf of Mexico and is especially abundant on the Great Lakes sand beaches, sand dunes, and dry sand plain (Evans 1950; Evans and Yoshimoto 1962; Kurczewski 1999, 2001; Kurczewski and Kiernan 2015). Episyron conterminus cressoni frequents sandy soils of the Atlantic Coastal Plain south of Long Island, Gulf Coastal Plain, Mississippi River Valley, and from California to Costa Rica (Krombein 1952; Kurczewski 1963; Evans 1966; Wasbauer and Kimsey 1985; Krombein and Norden 1996). Episyron b. biguttatus occurs from Canada to the Gulf of Mexico and nests in open woodland, woodland edges, overgrown fields, and vegetable gardens in loamy sand, gravel, and loam; abandoned gravel pits; and gravelly

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Figures 1–3. Habitus photographs of *Episyron* Schiødte females. **1)** *Episyron q. quinquenotatus* (Say) female habitus, Inverhuron Provincial Park, Bruce County, Ontario, Canada. Photograph © Robin McLeod. **2)** *Episyron conterminus cressoni* (Dewitz) female habitus, Natural History Museum of Los Angeles County gardens, Los Angeles County, California. Photograph © Hartmut Wisch. **3)** *Episyron b. biguttatus* (Fabricius) female habitus, Orange Town Forest, Orange County, Vermont. Photograph © Tom Murray.

parking lots (Kurczewski 1962, 1999; Kurczewski and Kiernan 2015). Difference in habitat between the three subspecies correlates with the extent of the female protarsal digging rake: *E. q. quinquenotatus* basitarsus has 4 or 5 flattened, very long comb spines; *E. conterminus cressoni* has 3 long comb spines; and *E. b. biguttatus* has 3 shorter comb spines. The comb spines of *E. b. biguttatus* are shorter than other Nearctic species of *Episyron*, including *E. oregon* Evans and *E. snowi* (Viereck) (Evans 1950).

Nearctic species and subspecies of *Episyron* capture and provision nests in soil with various genera and species of Araneidae (orb-weaving spiders) (Evans and Yoshimoto 1962). The females search for, approach, and attack the orb-weavers in their webs, usually causing the spider to drop to the ground where it is stung and immobilized (Kurczewski 2001). Although occupying different habitats, *E. q. quinquenotatus* and *E. b. biguttatus* have a remarkably similar list of host orb-weaving spiders, including seven common genera and nine common species in Erie County, PA (Kurczewski and Kiernan 2015). There is much less similarity in host genera and species of Araneidae between *E. q. quinquenotatus* and *E. conterminus cressoni*, despite likeness in habitat, because of their different geographic ranges and ecological regions (Krombein 1952; Kurczewski 1963, 1981; Kurczewski and Kurczewski 1968a, b, 1973; Krombein and Norden 1996). *Episyron q. quinquenotatus* predominantly inhabits the northeastern U. S. and *E. conterminus cressoni*, the southeastern U. S. (Evans 1950).

Materials and Methods

Field observations were made on the three *Episyron* subspecies from 1960 through 2014 in Ontario, New York, Pennsylvania, Michigan, New Jersey, Maryland, Florida, and California. The following number of females were observed, habitat noted, nests excavated, and host spiders identified: *E. q. quinquenotatus*, 446; *E. b. biguttatus*, 42; and *E. conterminus cressoni*, 33. Habitat and nesting behavior information was correlated with subspecies external morphology using dichotomous keys and subspecies descriptions in Evans (1950, 1951, 1966) and Wasbauer and Kimsey (1985). Ecological information on these subspecies was compared with reports by Krombein (1952), Evans and Yoshimoto (1962), Kurczewski (1962, 1963, 1981, 1999, 2001), Kurczewski and Kurczewski (1968a, b, 1973), Krombein and Norden (1996), Kurczewski and Pitts (2011), Kurczewski et al. (2013, 2017), and Kurczewski and Kiernan (2015).

Results and Discussion

The evolutionary development of a ground-nesting spider wasp species is related to many environmental factors: ambient temperature; amount of precipitation; daily hours of sunshine and cloud cover; density of vegetation; and soil friability, texture, temperature, and humidity. The conspicuousness of aposematic coloration within species and between congeners varies in Nearctic species of Pompilidae. The amount of warning coloration of spider wasp species or subspecies often infers the type of habitat and density of vegetation of the area. *Episyron q. quinquenotatus* and *E. conterminus cressoni* have an extensive amount of aposematic coloration and both species inhabit bare or sparsely vegetated sandy soils, often near water courses. *Episyron b. biguttatus* has much less warning coloration and inhabits areas with denser vegetation and often gravelly or loamy soil. [For example, compare Fig. 2 (*E. biguttatus*, abandoned and overgrown gravel pit) and Fig. 24 (*E. quinquenotatus*, sand beach and sand dunes) in Kurczewski and Kiernan (2015) for typical habitat and soil differences.] The larger number or length of comb spines on the protarsal digging rakes of *E. q. quinquenotatus* and *E. conterminus cressoni* reinforce their distinctive psammophilous habitats in contrast to the shorter comb spines and more densely vegetated, less friable soils of *E. b. biguttatus*.

Another example of the extent of aposematic coloration correlated with climate, habitat, and density of vegetation is found among the three subspecies of *Anoplius apiculatus* (Smith), also in the tribe Pompilini. The three subspecies designated by Evans (1951) are highly psammophilous, occurring mainly on sand beaches and sand dunes along water courses. In these taxa the 3 comb spines of the protarsal digging rake are exceedingly long, as in *E. q. quinquenotatus*. Noticeable differences between the three subspecies include the amount of rufous aposematic coloration on the metasomal segments and silvery pubescence on the body, which acts as reflective

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vestiture. Anoplius apiculatus apiculatus (Smith) occurs from the Lower Sonoran Region to Central America. It has a bright rufous metasoma, except for the small black base of the first segment (Evans 1951). The wings are hyaline in density and the reflective pubescence of the body is conspicuously silvery. This color combination is typical of certain solitary wasps (Hymenoptera: Aculeata) from open, sparsely vegetated, arid, or semi-arid terrain in southwestern U. S. and Mexico with low levels of annual precipitation and high summer temperatures. Anoplius apiculatus autumnalis (Banks) inhabits the Great Plains and Eastern Temperate Forest Level I Ecological Region of North America (Commission for Environmental Cooperation Working Group 2006). The most common aposematic coloration of the metasoma of this subspecies is basal 3 segments rufous and apical 3 segments black (Evans 1951). The body of A. apiculatus autumnalis is patterned with reflective silvery pubescence and the apical half to third of the forewing is lightly infuscate. This color combination is typical of Pompilini from the eastern U. S. in areas with denser vegetation, higher amount of annual precipitation, and more moderate summer temperatures. Anoplius apiculatus pretiosus (Banks) ranges from Maine to Florida in the Atlantic Coastal Plain. This subspecies has noticeably darker body coloration than A. apiculatus autumnalis, silvery pubescence substantially reduced, and forewing more fuscous (Evans 1951). Darker body coloration is typical of wasp populations that live along the Atlantic Coast, especially in the southeastern U. S. Areas along the ocean generally stay cooler and have a more moderate temperature range than inland areas, lessening the need for reflective silvery body pubescence that prevent overheating.

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