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Sexual Dimorphism Of Wasp Antennal Structure in Relation to Parasitic and Non-parasitic Behavior (Hymenoptera: Sphecidae)

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Abstract.—To assess the relationship between sensory ecology and behavior of non-parasitic and parasitic spheciforme wasps (Sphecidae), I measured the lengths of scapes, flagella, and body size (intertegular distance) of males and females of 29 species, representing 7 subfamilies and 26 tribes. Unlike a previous study with bees (Wcislo, 1995), spheciforme wasps show no consistent sexual dimorphism in relative antennal size for free-living versus parasitic species.

Brood parasitism (cuckoo behavior) and social parasitism have evolved repeatedly among bees, aculeate wasps and ants (e.g., Wcislo 1987; Wcislo and Cane 1996; Hölldobler and Wilson 1990; Cervo and Dani 1996). Parasites utilize host-derived resources (a nest, stored food, or worker labor) to rear their own offspring. Maternal behavior of parasitic and non-parasitic species differs (Wcislo 1987), while respective males do not differ essentially in mating behavior, although data are scant (e.g., compare Cederberg et al. 1984 with Alcock and Alcock 1983). Few studies have investigated the sensory ecology (*sensu* Dusenbury 1992) of parasitic and non-parasitic Aculeata to ascertain if differences in sensory structures co-occur with behavioral differences. Non-parasitic bees (Apoidea) usually are strongly sexually dimorphic for antennal structures; at a given body size, males tend to have shorter scapes and longer flagella (Wcislo 1995; Müller 1872). Parasitic bees, in contrast, usually are not sexually dimorphic for relative size of antennal structures. Among ants, a fusion of antennal flagellomeres is part of a syndrome of structural characters associated with parasitic behavior (Hölldobler and Wilson 1990).

Some clades of spheciforme wasps (= "Sphecidae" of Bohart and Menke 1976) together with the bees form a monophyletic group, Apoidea (e.g., Alexander 1992; Brothers and Carpenter 1993). Parasitism has evolved repeatedly in bees (e.g., Wcislo and Cane 1996), and has probably evolved twice among spheciforme wasps, once in the common ancestor of the genus *Stizoides* and once in the common ancestor of Nyssonini (see Bohart and Menke 1976). Thus, the evolution of parasitism among sphecid wasps provides additional examples to assess whether female parasites are similar to males in their sensory ecology and relevant structures. This note presents information on antennal size for parasitic and non-parasitic wasps (Sphecidae), as part of an on-going comparative study of the relationship between morphological and behavioral evolution within aculeate Hymenoptera (cf. Wcislo 1989).

MATERIALS AND METHODS

In an effort to minimize phylogenetic bias I used 29 species, representing 7 subfamilies and 26 tribes of the 10 subfamilies and 30 tribes that Menke (1997) lists for Sphecidae (see Appendix). Intertegular distances, scape length, pedicel length,

and total flagellar length was measured on 5 individuals of each sex using methods in Wcislo (1995). Values are reported as means with standard errors. Data were analyzed using SYSTAT (Wilkinson 1988) on a personal computer, unless otherwise indicated. Phylogenetic bias probably exists within these data due to nonindependence of the taxa (e.g., Harvey and Pagel 1991). There is, however, no widely-accepted phylogenetic hypothesis available for the taxa included here, and taxonomy may be a poor indicator of phylogeny (see discussion in Alexander 1992).

RESULTS

Parasitism is relatively rare among spheciforme wasps. Among non-parasitic species males and females, on average, were not significantly different in body size (mean intertegular distance in mm: females, 1.95 ± 0.17; males, 1.66 ± 0.15; Mann-Whitney U = 402.5, P > 0.2). The sexes did not differ in mean length of the flagella (in mm, females: 3.44 ± 0.46; males: 3.28 ± 0.39; Mann-Whitney U = 348, P > 0.8) (Figure 1, bottom). Males had significantly smaller mean scape length than females (in mm, females: 0.55 ± 0.053; males: 0.43 ± 0.04; Mann-Whitney U = 461, P = 0.02; Figure 1, top). Within species, non-parasitic females more frequently had a larger body size than males (two-tailed sign test, P < 0.05, T = 22, N = 26), and had longer scapes (two-tailed sign test, P < 0.05, T = 23, N = 23), but females did not have longer flagella (two-tailed sign test, 0.1 > P > 0.05, T = 17, N = 25) (sample sizes differ because ties were eliminated; Conover 1971). Regression equations for non-parasitic males versus females were not significantly different for scape or flagellum length as a function of body size (P > 0.05, comparing y-intercepts or slopes). Male and female parasites did not differ in body size, nor in lengths of scapes and flagella.

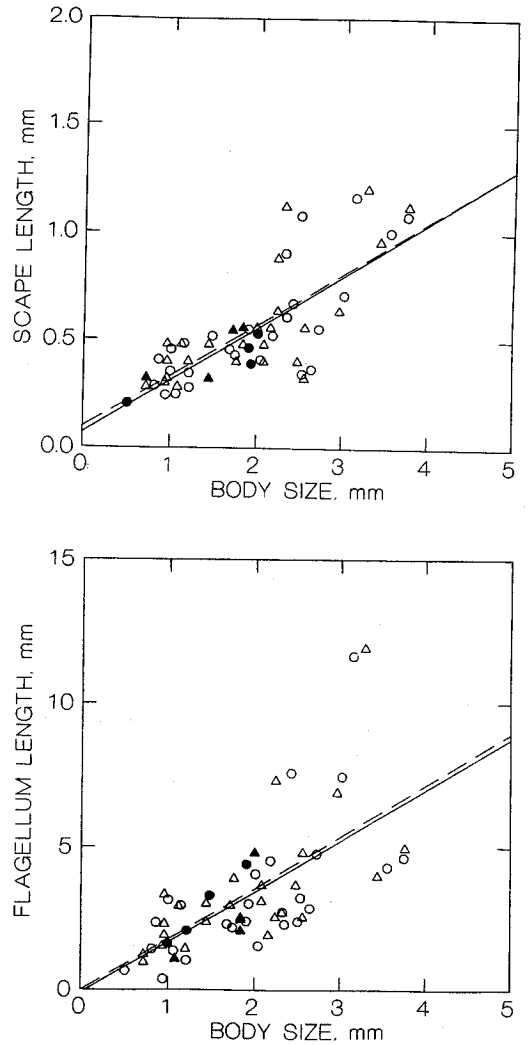

Fig. 1. Scape (top) and flagellum (bottom) length of spheciforme wasps as a function of body size (intertegular distance). Open circle = non-parasitic female; open triangle = non-parasitic male; closed circle = parasitic female; closed triangle = parasitic male.

DISCUSSION

Among non-parasitic spheciforme wasps females often are larger than males, and have longer scapes. Small samples preclude statistical analyses, but parasitic females are not conspicuously larger than conspecific males, and have similarly sized scapes and flagella. In contrast, a study of 114 bee species showed that 1) female non-parasitic bees of a given body size have

longer scapes but shorter flagella than conspecific males, and 2) for parasitic bees, scapes and flagella are similar in size, on average, between males and females of a species (Wcislo 1995; also Müller 1872). Since bees are closely related to, and probably arose from within spheciforme wasps (e.g., Alexander 1992), the sexual differences are probably derived among bees. Relative to non-parasitic females, female parasites may be more "male-like" in their search behavior, but pertinent data are scarce (refs. in Wcislo 1995). If substantiated, these behavioral differences can help explain similarities in sensory structures among males of parasitic and non-parasitic species and females of parasitic species, which differ from non-parasitic females.

Antennae have olfactory, gustatory, and tactile sensory receptors; they are used like calipers during nest construction; and they can be used to drum, tap, or stroke parts of the female's body (refs. in Wcislo 1995). The scape of some male spheciforme wasps is broadly expanded (e.g., *Dinetus*), like males of a parasitic bee, *Doeringiella* (Roig-Alsina 1989); these expansions may house glands for use during courtship and mating, as known for other Hymenoptera (Isidoro et al. 1996). The functional morphology of antennae has been studied for relatively few species, and typically only for one or two sensory modalities. Antennae have multiple functions, highlighting the need for more detailed studies relating behavior to an animal's sensory world (*"umwelt"*), as pointed out long ago by von Uexküll (1934).

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APPENDIX

List of spheciforme wasp species from which antennal measurements were taken. * = parasitic taxon; ? = taxon is probably parasitic, but behavioral data are unavailable. Nomenclature follows Bohart and Menke (1976), as modified by Menke (1997).

AMPULICINAE

AMPULICINI

Ampulex compressa (Fabricius)

DOLICHURINI

Dolichurus corniculus (Spinola)

ASTATINAE

DINETINI

Dinetus pictus (Fabricius)

ASTATINI

Astata mexicana Cresson

PHILANTHINAE

EREMIASPHECIINI

Eremiasphecium schmiedeknechtii Kohl

APHILANTHOPSINI

Aphilanthops frigidus (Smith)

PHILANTHINI

Philanthus solivagus Say

CERCERINI

Cerceris frontata Say

PEMPHREDONINAE

PSENINI

Psenulus pallipes (Panzer)

PEMPHREDONINI

Stigmus americanus Packard

SPHECINAE

AMMOPHILINI

Ammophila polita Cresson

SCELIPHRONINI

Podium rufipes Fabricius

SPHECINI

Sphex dorsalis (=*singularis*) Smith

BEMBICINAE

HELIOCAUSINI

Heliocausus larroides (Spinola)

MELLININI

Mellinus arvensis (Linnaeus)

STIZINI

Bembicinus wheeleri Krombein & Willink
**Stizoides unicinctus* (=*renicinctus*) (Say)

GORYTINI

Gorytes simillimus Smith

*NYSSONINI

**Nysson (Epinysson) mellipes* (Cresson)
**?Synnevrus aequalis* (Patton)
**Nysson simplicicornis* Fox

BEMBICINI

Bembix texana Cresson

CRABRONINAE

LARRINI

Larra bicolor Fabricius

MISCOPHINI

Solierella plenoculoides (Fox)

PALARINI

Palarus latifrons Kohl

TRYPOXYLONINI

Trypoxylon lactitarse Saussure

SCAPHEUTINI

Scapheutes brasilianus Handlirsch

CRABRONINI

Crabro cribrellifer (Packard)

OXYBELINI

Oxybelus emarginatus Say