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PROC. ENTOMOL. SOC. WASH.
88(4), 1986, pp. 628–633

REPRODUCTIVE AND NESTING BIOLOGY OF *BEMBECINUS NANUS STRENUUS* (MICKEL) (HYMENOPTERA, SPHECIDAE)

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Abstract.—A population of *Bembecinus nanus strenuus* was studied in a blowout among dunes near Roggen, Weld County, Colorado. Males fly over the emergence and nesting area in irregular patterns and respond to small, dark objects, including conspecifics, on the soil surface. Males intercept post-emergent females perching on the sand, some of which have already begun nesting, and copulation occurs, lasting several seconds. Little aggression between males was observed. Nests of females are unicellular, 9 to 16.5 cm deep, and are provisioned progressively with insects of three families of Homoptera (Cixiidae, Dictyopharidae, Cicadellidae). A comparative discussion of the reproductive biology of males and females of this species and *B. quinquespinosus* is included.

The major details of the biology of digger wasps of the genus *Bembecinus* are relatively well known (reviews in Evans, 1955, 1966). One obtains the impression that there is little behavioral variation among the species of this genus. Recently, we had an opportunity to study populations of two species that occur in abundance at localized sites in Weld County, Colorado. We have reported on one of these, *B. quinquespinosus* (Say), elsewhere (O'Neill and Evans, 1983; Evans et al., 1986). We take the opportunity here to report on the second species, *B. nanus strenuus* (Mickel), and to point out several differences in the biology of the two species. With respect to color, *B. nanus* is a monomorphic species, both sexes being black with narrow, pale bands on the abdomen. In contrast, *B. quinquespinosus* is polymorphic in the male sex, larger males being almost entirely yellow, small males (like the females) being black with pale bands; males of intermediate size are intermediate in coloration (Krombein and Willink, 1951; O'Neill and Evans, 1983).

There are no published reports of *B. nanus strenuus,* but Shappirio (1946) found an aggregation of the eastern subspecies, *B. nanus nanus* (Handlirsch), in Washington, D.C., and presented brief notes on the nest provisioning. The prey consisted of leafhoppers and a species of Fulgoroidea. It is probable that Bridwell's (1937) report of *B. moneduloides* (Smith) from Virginia also applies to *B. n. nanus,* the only species of the genus occurring in that area. Bridwell found a cocoon surrounded by the remains of 15 Homoptera of 8 species belonging to the families Cicadellidae, Membracidae, Cercopidae, Acanaloniidae, and Cixiidae. The use of

a variety of Homoptera is consistent with our observations of *B. n. strenuus* in Colorado.

Our studies were conducted in a blowout in sand dunes near Roggen, Colorado, where these wasps have been abundant at least since 1974. The wasps occupied a broad area, measuring about 5 by 12 m, on a gentle slope sparsely vegetated with grasses and scurfpea, *Psoralea lanceolata* Pursh. Studies of another digger wasp *Philanthus psyche* were conducted at this site (O'Neill, 1979, 1983), and, in fact, the nests of the two species were intermingled. *B. nanus strenuus* is active primarily through the month of July; our studies were made intermittently 6–30 July 1982–1985.

Reproductive Behavior

During the early part of the day (0800–1300) up to several hundred males flew in irregular patterns several m long and 2–5 cm high, but rising to 30 cm to pass over plants. Males sometimes pursued other insects flying close to the ground, such as male Mutillidae. While individually marked males were found to remain for the most part within a few meters of the same site, there was no observed tendency for males to defend a specific area. Between flights males perched briefly on the ground, the duration of perches decreasing markedly as surface and air temperature increased during the day; surface temperature varied between 25° and 54°C during the activity period. There was a significant negative correlation between sand surface temperature (measured with a Model 870 Keithley digital thermocouple thermometer) and the duration of perches between patrolling flights ($r = -0.54$; $N = 146$; $P < 0.001$). On 8 July, 1984 at 1015, when the surface temperature reached 46°C, males began to perch between some flights on scurfpea plants rather than on the surface; by 1115, when the surface temperature had reached 54°C, males perched only on plants. In contrast to *B. quinquespinosus,* where only large males were active at high temperatures (O'Neill, unpublished data), the body size of males active (sampling without replacement) between surface temperatures of 26° and 52°C was not correlated with these temperatures ($r = -0.04$; $N = 100$; $P = 0.68$).

Males also interact frequently with conspecifics (or objects resembling the dark-colored conspecifics). They pounce upon various dark objects of about their own size on the sand. Pale, immature grasshoppers were abundant at the site, but generally elicited no response; however, males did occasionally drop onto darker colored grasshoppers, *Dactylotum bicolor* Thomas. In an effort to quantify the males' preference for darker colored objects, we prepared a series of small wooden cylinders, 15 mm long by 4 mm in diameter, painted with 6 colors of Testor's gloss enamel paints®. These were glued to a board 5 cm apart and parallel to one another; the board was placed on the sand with only the wooden cylinders exposed. Males flying over the area struck or landed upon the black cylinder significantly more often than on the other colors ($\chi^2_5 = 460.4$; $P < 0.0001$). The following is the frequency of responses to the six colors over one hour (0900 to 1000) on 9 July 1985: orange, 24; green, 9; white, 0; black, 125; yellow, 0; blue, 0.

In contrast, an identical series of observations undertaken on *B. quinquespinosus* on 16 July 1985, between 0900 and 1000, gave the following pattern of responses: orange, 11; green, 36; white, 1; black, 7; yellow, 6; blue, 0. Although this also represents a non-random pattern ($\chi^2_5 = 86.8$; $P < 0.001$), there was no tendency

for a biased response towards black. The potential significance of this will be discussed later.

On 15 occasions we saw males of *B. nanus* descend upon females perched upon the sand surface; in 7 of these instances, this resulted in matings lasting only 3 to 5 seconds. Males sometimes descended upon females working at nest entrances, and on one occasion apparently mated successfully with such a female, although on 8 others the females rejected the male, usually with a vigorous struggle, after contact was made. Other females flew off as patrolling males approached them.

Males displayed little overt aggression toward one another. They frequently pounced upon perched males during patrolling flights, but the duration and form of these interactions suggest that they were misdirected copulation attempts, rather than aggressive interactions. Flying males also approached one another within several cm, briefly hovering face-to-face without making contact. Only one male was present in 87% of 15 observed copulation attempts and mating was usually completed *in situ* without interference. In the two cases in which more than one male was present, the interactions were short-lived and not of the intensity usually observed in *B. quinquespinosus* (O'Neill and Evans, 1983). Once two males attempted copulation at the same time, but the larger of the two displaced the smaller and mated with the female. On another occasion, 4 males formed a cluster around a female; one emerged with the female, but had difficulty flying with the female, which was larger, and mated only a short distance away. Thus, the mating tactics of *B. nanus* are generally in the form of a scramble competition, although interference competition occasionally occurs.

Nesting Behavior

Females nested in the same area from which they had emerged and over which the males patrolled. Sand is removed from the burrow with simultaneous movements of the forelegs and allowed to form a small mound at the entrance. From time to time, the female backs across the mound and moves forward in a somewhat zig-zag pattern, partially dispersing the sand. Burrows are oblique, 16–25 cm long, reaching a cell at its terminus at a depth of 9–16.5 cm (mean = 13.5, N = 12). Burrows are straight or nearly so, and nests are unicellular. As in other species of the genus, the egg is laid in the empty cell on top of several grains of sand, sloping away from the entrance, and prey are brought in progressively over the next several days. Nests in this area were well-dispersed, usually at least 30 cm apart. At one site, measuring 60 cm^2, near the center of the nesting area, we sifted the soil, but found only 4 cocoons.

Combined prey from several nests consisted of a variety of Homoptera, as follows:

Cixiidae: *Oecleus excavatus* Ball, 2 adults
Dictyopharidae: *Scolops maculosus* Ball, 9 adults
Scolops sp., 34 immatures
Cicadellidae: 16 adults of 9 species; also 10 immatures
Cicadellinae
Carneacephala sp., probably *gillettei* Ball, 1 male
Cuerna striata (Walker), 2 females, 2 males
Draeculacephala sp., 1 female

Agalliinae
Aceratagallia sp., probably *sanguinalenta* (Prov.), 2 females
Hecalinae
Dicyphonia ornata (Baker), 2 females
Deltocephalinae
Acinopterus viridis Ball, 2 females, 1 male
Athysanella wilburi Ball and Beamer, 1 male
Flexamia inflata Osborn and Ball, 1 female
Mesamia sp., probably *nigridorsum* (Ball), 1 female

Discussion

The two species of *Bembecinus* that we have studied in northeastern Colorado contrast markedly with respect to male mating strategies. In *B. quinquespinosus* the male color polymorphism correlates with alternative mating tactics. The extensively yellow males compete vigorously before and after digging emerging females from the soil; the smaller, darker males are generally found to patrol the area adjacent to the emergence area and attempt to mate with females that elude attempts of the larger males (O'Neill and Evans, 1983 and unpublished data). The latter tactic is essentially identical in form, though not in location, to the only mating tactic that we identified for *B. nanus strenuus*; this form of male mating activity has been commonly observed in the subfamily Nyssoninae (Evans, 1966). The fact that males of *B. nanus* search for black "objects" upon the sand, while males of *B. quinquespinosus* respond to the presence of groups of digging conspecific males which are yellow may explain the species differences in response to our colored cylinders in the observations described above. Males of the former species may thus be reacting to the presence of a potential mate (black), while those of the latter are responding to males that gather at the potential emergence site of a female. Presumably the green paint we used had reflectance properties similar to the greenish-yellow of the larger males.

The two species also differ with respect to the degree of sexual size dimorphism, another trait that appears to be related to differences in male mating tactics. While in *B. quinquespinosus* males and females have the same mean size and size range (O'Neill and Evans, 1983), females of *B. nanus strenuus* (mean head width = 2.60 mm, SD = 0.20, N = 47) are significantly larger than males on average (mean male head width = 2.37, SD = 0.15, N = 123; *t*-test, $t_{163} = 9.81$, $P < 0.001$). The latter is typical of digger wasps in general (O'Neill, 1985). In the former species, the result is that the large yellow males in the emergence area are usually larger than emerging females. This allows them to more easily lift and carry females in flight in order to escape the usually intense competition (O'Neill and Evans, 1983 and unpublished data). On the other hand, since males of *B. nanus* usually find females without conspecific male competitors present, carrying the female away from the emergence area would usually accrue little advantage in terms of increased mating success. Thus, in contrast to *B. quinquespinosus,* there may be little selection pressure for larger relative body size in *B. nanus.*

In *B. quinquespinosus,* females nest at a different site each year, while maintaining the integrity of their dense aggregations. These sites may be 100 m apart in consecutive years. We have suggested elsewhere that this movement is a re-

sponse to harassment by males of females attempting to nest in the emergence area while searching males are still present (Evans et al., 1986). On the other hand, the population of *B. nanus strenuus* we studied has nested in the same place for several consecutive years, presumably a reflection of the more diffuse nests and the lower male density, resulting in less harassment of nesting females.

In contrast to the diversity of prey used by *B. nanus strenuus,* the population of *B. quinquespinosus* we studied (O'Neill and Evans, 1983; Evans et al., 1986) preyed exclusively upon Cicadellidae of two species, *Cuerna striata* (Walker), 121 adults, and *Amphigonalia* sp. near *gothica* (Signoret), 13 adults (both Cicadellinae), plus 623 immature Cicadellidae (probably of these same two species). Nests were similar to those of *B. nanus strenuus* though dug in much coarser sandy gravel; cell depth varied from 8 to 12 cm (mean = 9.9, N = 8). Neither species makes accessory burrows as described for certain Australian species (Evans and Matthews, 1971). Nest density differs greatly in the two species, nests of *B. quinquespinosus* often being only 5–10 cm apart, such that burrows are closely adjacent and may intersect.

It appears that most species of *Bembecinus* employ Homoptera of diverse groups; thus exclusive use of Cicadellidae may be a specialization. Other published records for *B. quinquespinosus* (under the name *godmani*) confirm its restriction to Cicadellidae (review by Evans, 1955). Only the South American species *B. agilis* is also reported to specialize on Cicadellidae (Richards, 1937, under the name *cingulatus*). On the other hand, not only *nanus,* but three European, three Australian, and three Asiatic species are known to each use a variety of homopteran families (Evans, 1955; Evans and Matthews, 1971; Krombein, 1984). Two anomalous, turret-building South African species use both Homoptera and Diptera as prey (Gess, 1975).

It seems safe to categorize *B. nanus* as a relatively generalized member of the genus with respect to its reproductive behavior; it possesses traits typical of most *Bembecinus* in particular and many nyssonines in general. On the other hand, *B. quinquespinosus* exhibits many derived behavioral and morphological traits: the females specialize on cicadellid leafhoppers and move their nesting area each year, the males have a unique color polymorphism, are the same average size as females, and possess rudimentary rake spines on their forelegs that may aid in digging for females (O'Neill and Evans, 1983). It must be pointed out that these differences are based upon one population of each species studied at different localities in Colorado. Other published observations (Evans, 1955) on these species do not contradict these statements, but at this point it would be premature to maintain that species differences are consistent throughout their respective ranges, particularly with regard to relatively labile behavioral traits.

Acknowledgments

We thank Paul H. Freytag, of the University of Kentucky, and H. Derrick Blocker, of Kansas State University, for identifying the Cicadellidae; also Stephen W. Wilson, of Central Missouri State University, for identifying the *Scolops*. Ruth O'Neill provided assistance with the field work.

Literature Cited

Bohart, R. M. and A. S. Menke. 1976. Sphecid wasps of the world. Univ. Calif. Press, Berkeley, CA. 695 pp.

Bridwell, J. C. 1937. Report on *Bembecinus moneduloides* (Smith). Proc. Entomol. Soc. Wash. 39: 14–15.

Evans, H. E. 1955. An ethological study of the digger wasp *Bembecinus neglectus,* with a review of the ethology of the genus. Behaviour 7: 287–303.

———. 1966. The comparative ethology and evolution of the sand wasps. Harvard Univ. Press, Cambridge, MA. 529 pp.

Evans, H. E. and R. W. Matthews. 1971. Nesting behaviour and larval stages of some Australian nyssonine sand wasps (Hymenoptera: Sphecidae). Austr. J. Zool. 19: 293–310.

Evans, H. E., K. M. O'Neill, and R. P. O'Neill. 1986. Nesting site changes and nocturnal clustering in the sand wasp *Bembecinus quinquespinosus* (Hymenoptera: Sphecidae). J. Kans. Entomol. Soc. 59: 280–286.

Gess, F. W. 1975. Ethological studies of *Bembecinus cinguliger* (Smith) and *B. oxydorcus* (Handl.) (Hymenoptera: Sphecidae), two southern African turret-building wasps. Ann. Cape Prov. Mus. (Nat. Hist.) 11: 21–46.

Krombein, K. V. 1984. Biosystematic studies of Ceylonese wasps, XIII: A monograph of the Stizinae (Hymenoptera: Sphecoidea, Nyssonidae). Smithson. Contr. Zool. 388: 1–37.

Krombein, K. V. and A. Willink. 1951. The North American species of *Bembecinus* (Hymenoptera, Sphecidae, Stizini). Am. Midl. Nat. 44: 699–713.

O'Neill, K. M. 1979. Territorial behavior in males of *Philanthus psyche* (Hymenoptera: Sphecidae). Psyche 86: 19–43.

———. 1983. The significance of body size in territorial interactions of male beewolves (Hymenoptera: Sphecidae, *Philanthus*). Anim. Behav. 31: 404–411.

———. 1985. Egg size, prey size, and sexual size dimorphism in digger wasps (Hymenoptera: Sphecidae). Can. J. Zool. 63: 2187–2193.

O'Neill, K. M. and H. E. Evans. 1983. Alternative male mating tactics in *Bembecinus quinquespinosus* (Hymenoptera: Sphecidae): Correlations with size and color variation. Behav. Ecol. Sociobiol. 14: 39–46.

Richards, O. W. 1937. Results of the Oxford University Expedition to British Guiana, 1929. Hymenoptera, Sphecidae and Bembicidae. Trans. R. Entomol. Soc. Lond. 94 pp.

Shappirio, D. G. 1946. Notes on District of Columbia wasps (Hymenoptera: Sphecidae). Entomol. News 57: 229–230.