The Behavior of *Microbembex nigrifrons*
(Hymenoptera: Sphecidae)

JOHN ALCOCK AND ALLEN F. RYAN
Department of Zoology, Arizona State University, Tempe, 85281, and Departments of Psychology, Physiology, & Biophysics, University of Washington, Seattle, 98195

The behavior of only a few species of *Microbembex* has been reported in any detail (Evans, 1966, for *M. monodonta* (Say); Goodman, 1970, for *M. californica* Bohart). This paper describes the behavior of a previously unstudied member of the genus, *M. nigrifrons* (Provancher). Over two summers (1971, 1972) we made a series of observations on this species in central Washington. The study site was located approximately five miles south of Interstate 10 on Dodson Road within ten miles of Royal City. A series of low dunes scattered through this area are inhabited by *M. nigrifrons* and other bembicine wasps. The dunes rise out of a flat plain covered with sage and other desert scrub brush with buckwheat (*Eriogonum sp.*) common on the fringes and crests of some dunes.

NESTING BEHAVIOR.—This species of *Microbembex* is extremely similar behaviorally to *M. monodonta, M. californica*, and all the South American species studied by Evans (personal communication). It nests primarily on the lower fringes of sand dunes and sand banks often burrowing into a slope. Upon completion of a burrow, a task that may require two to three hours early in the season (June), the female performs an initial closure similar to that described for *M. monodonta* by Evans (1966: 370). The wasp walks quickly away from the entrance kicking sand back toward the burrow. After going out 15–25 cm, it then returns and repeats the process in another direction over and over again until the nest is surrounded by a series of radiating lines. The burrow often, but not always, descends at a shallow angle for about one-half its length and then drops much more steeply before levelling off just before the cell (Fig. 1). All nests excavated were single celled.

The egg is laid upright in a vertical position in the empty cell. (One nest held an egg and one small dead beetle.) Provisioning females apparently select any dead arthropod available: ARACHNIDA: Scorpionida 1 (the tail), Araneida 5; INSECTA: Ephemeroptera 3, Orthoptera 15, Hemiptera 8, Neuroptera 1, Trichoptera 1, Lepidoptera 12 (adult and larval forms), Diptera 24, Hymenoptera 15, Coleoptera 31

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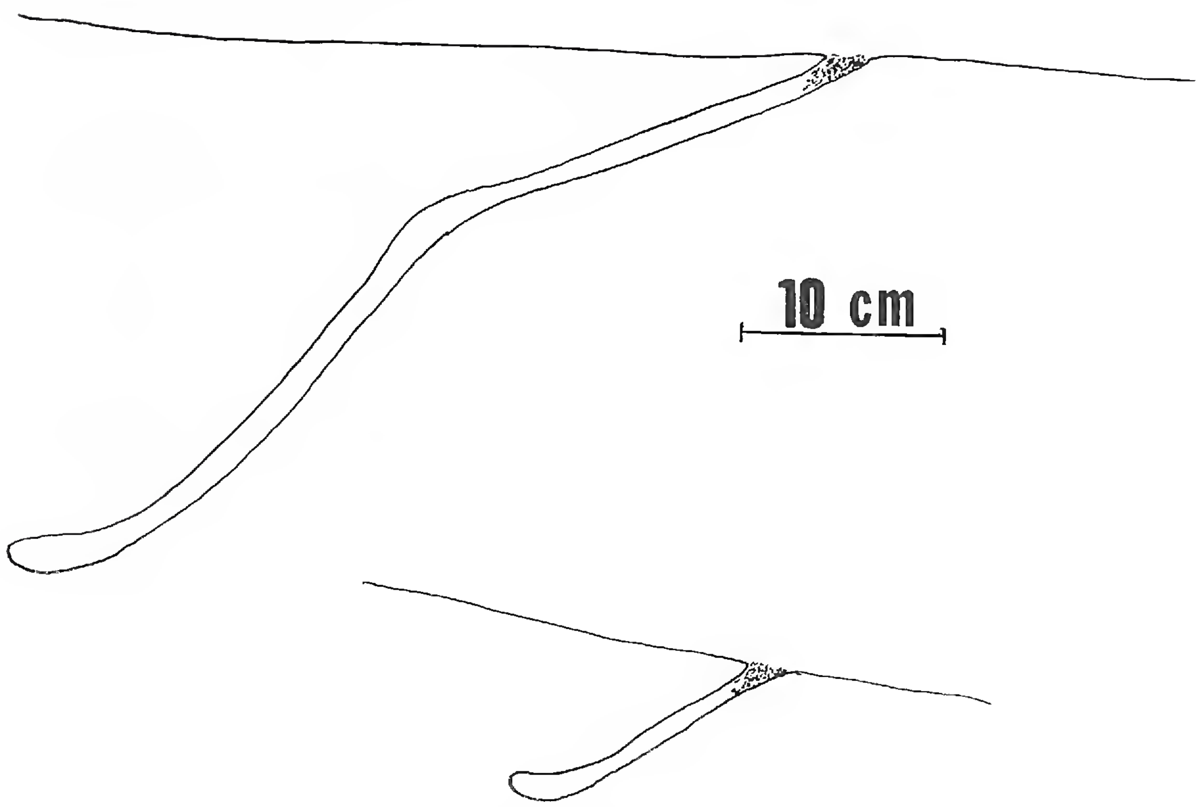

Fig. 1. A diagram of two nests of *M. nigrifrons* illustrating the variation in length and depth as well as nest design that existed at the Dodson Rd. site.

(adult and larval forms). In addition a few females were seen hovering over and then touching small brown seeds and other bits of dried vegetable material perhaps inspecting them as possible prey items.

Three females were observed shortly after they had taken a food item. Two clung upside down to the underside of a branch in the dunes rearranging the prey prior to flying back to the nest. The other was oriented vertically head down on a stick. Females returning to the nest were harassed by other members of their species and one successful prey stealing was observed. The average interval ($N = 8$) between provisioning trips to the nest was 21 minutes (range = 7–44). In every respect the behavior of *M. nigrifrons* is highly similar, if not identical, to that of *M. monodonta.*

Nest dimensions and sand moisture.—Evans (1966) noted considerable variation in cell depth and burrow length both at the same site and between nesting locations. He demonstrated that part of the differences between burrows was related to the size differences between females. Moreover, Evans speculated that variation between locations could be due to differences in the moisture content of the sand noting that the deepest nests were found in very dry Kansas dunes.

Because preliminary excavations of some nests in mid 1971 revealed exceptionally long and deep burrows this aspect of nesting behavior

TABLE 1. The relation between the nest dimensions of *M. nigrifrons* and the depth of moist sand in the dunes.

	10 June	12 July	12 August 1972	14 Sept. 1971
Average depth of moist sand (cm below surface)	5	11	17.5	5
Nests excavated	12	12	10	10
Average burrow length (cm)[1]	28.3	31.4	48.5	18.7
Range	(15–63)	(26–40)	(42–57)	(14–35)
Average cell depth (cm)[2]	13.4	18.9	31.8	14.0
Range	(11–23)	(14–23)	(25–38)	(9–20)
Average distance between moisture line and cell (cm)[3]	10.3	8.1	14.3	9.0

[1] Correlation of burrow length with average depth of moist sand, $r = .76$, $P < .01$.
[2] Correlation of cell depth with average depth of moist sand, $r = .54$, $P < .01$.
[3] F test of mean depths of cells below moisture line, $F_{(3,40)} = 16.8$, $P < .01$.

was chosen for more study. On four occasions (14 September 1971, 10 June, 12 July and 12 August 1972) a sample of 10–12 nests was excavated. In the Dodson Road dune area the moisture level in the dunes was very clear cut; extremely dry loose sand gave way to moist compact sand anywhere between 3.5–20 cm beneath the surface depending on the time of year. Table 1 presents data on the correlation between average depth of moist sand and the dimensions of the nests. It is abundantly clear that the lower the moisture level, the deeper and longer the burrows.

The adaptive significance of this behavior is not obscure. It is to the wasp's advantage to locate its cell in an area where the egg and larva will not desiccate prior to formation of a cocoon. This response does indicate a degree of behavioral flexibility with wasps in this population capable of constructing a burrow anywhere from 14–63 cm long depending on environmental conditions. But even this variation can be readily achieved if the wasp is simply programmed to dig a nest with the cell about 10 cm beneath the moisture line (approximately 80% of the sample had cells 7–15 cm below the line). However, the matter is somewhat more complex than this. Wasps building nests when the moisture level was very low placed their cells significantly deeper below the line than those nesting when moist sand was closer to the surface of the dunes (Table 1).

ORIENTATION TO THE NEST.—Evans (1966) remarks that *M. mono-*

donta exhibits an astonishing ability to locate its nest entrance despite great disturbance to the surrounding terrain. He describes experiments by himself and others in which landmarks close to and far from the nest were moved without affecting the orientation of the wasp in the slightest.

We report here a very simple experiment on the homing ability of *M. nigrifrons.* It was apparent from casual observation that females had no difficulty finding their nest although the sand over and around the entrance might be very much disturbed by our activities. To test landmark learning by this species a ring of whitish stones 2–3 cm in diameter were placed in a circle about 15 cm from a nest entrance on 9 August 1972. In addition, a twig 8 cm long was placed inside the ring. The female was digging the nest when this was done.

On 12 August an observer returned to the site to find that there were now two females nesting inside the ring. The stones and twig were moved 25 cm to one side. A small grey pebble was placed where the twig had been to mark the location of the burrows for the benefit of the observer. The depressions left by the small stones were covered with fine sand.

One female returned with prey from her first provisioning trip after displacement of the landmarks and flew directly to the displaced ring. There she began to dig at a spot within the ring that corresponded to the site where the entrance would have been had the rocks not been moved. After 10 minutes of alternately digging and flying up, the female left the ring and flew to the true nest entrance. After digging there only briefly, she returned to the displaced ring, dug for a short time, flew back to the true nest site, opened the burrow and entered. Upon leaving the nest the wasp performed an elaborate and prolonged closure similar to an "initial closure." Five minutes later, she returned with another food item. The wasp flew directly to the displaced ring and dug there briefly before flying to the actual nest which she opened and entered. Nest closure was performed normally. On her third provisioning trip, the female went directly to the nest entrance and entered the burrow. Nest closure was normal.

The second female, returning from her first provisioning trip following displacement of the landmarks, went straight to the spot in the displaced ring where her entrance would have been had the stones not been moved. After about 5 minutes of digging, she flew to her true burrow and began work there. Like the other wasp, she returned to the ring and made several trips back and forth before finally opening the burrow and entering. Nest closure was performed normally.

It seems clear that *M. nigrifrons* will use landmarks close to the nest to locate the entrance. When these cues are very conspicuous it is possible to disorient the wasp by moving them. However, the effect is only temporary, unlike the permanent inability of *Philanthus triangulum* L. to find its nest when a ring of pine cones was displaced some distance from the entrance (Tinbergen, 1951). It may be that *M. nigrifrons* learns a variety of cues and can rely on alternate landmarks if major ones are removed or displaced.

The fact that the first female appeared to be more disoriented than the second one (digging for a longer period of time at the false nest site and performing an elaborate closure once the real nest had been found) is interesting. It seems probable that the second wasp had built her nest after the first one and therefore may have been less accustomed to and dependent upon the ring of stones as orientation guides. Much more work is necessary on this aspect of *Microbembex* behavior.

Acknowledgments

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RECENT LITERATURE

CERAMBYCIDAE OF NORTH AMERICA. PART VI, NO. 1. TAXONOMY AND CLASSIFICATION OF THE SUBFAMILY LEPTURINAE. E. Gorton Linsley and John A. Chemsak. University of California Publications in Entomology. Volume 69. University of California Press, Berkeley. 138 p., 41 figs., 2 plates. 1972. $5.50.

This volume is part of a continuing series toward a monograph of the long-horned beetles of America north of Mexico. It treats the tribes Desmocerini, Necydalini, and the 22 genera of Lepturini with lateral spines or tubercles on the pronotum and/or with entire eyes. Those Lepturini without pronotal tubercles and emarginate eyes will be treated subsequently in a second number of Part VI. Exquisite halftone illustrations by Celeste Greene and distribution maps are provided for many representative species.—ROBBIN W. THORP, *University of California, Davis, 95616*