

Communal Nesting in a North American Pearly-Banded Bee, *Nomia tetrazonata*, with Notes on Nesting Behavior of *Dieunomia heteropoda* (Hymenoptera: Halictidae: Nomiinae)

WILLIAM T. WCISLO¹

Center for Insect Science, University of Arizona, Tucson, AZ 85721

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ABSTRACT Information on the biology of the ground-nesting bee, *Nomia tetrazonata* Cockerell, provides the first documentation of large, multifemale nests in a North American nomiine bee. Females nest in aggregations of loosely clumped nests, and from 1 to at least 20 females actively provision cells in a single nest on the same days. Nests are parasitized by a cuckoo bee, *Triepeolus verbesinae* (Cockerell) (Nomadinae), but parasitism rates are low (<2%). Information is also given on nest architecture, provisioning behavior, and diel and seasonal activity. Comparable information is also provided for a solitary species, *Dieunomia heteropoda* (Say), females of which are pollen specialists on *Helianthus petiolaris*. The provision masses of these mostly solitary bees are parasitized by another cuckoo bee, *Triepeolus distinctus* (Cresson). The discussion summarizes behavioral data on nomiine bees which may provide useful systematic characters.

KEY WORDS Sociality, nest architecture, *Triepeolus* spp.

BEES IN THE family Halictidae are excellent for studying the causes and consequences of social evolution. Most studies have focused on Halictinae (reviewed by Michener 1990a); the biology of bees in the Rophitinae and Nomiinae is less well known. In North America, bees in the latter subfamilies are generally assumed to be solitary. A few cases of group living behavior have been reported for Old World species (see Discussion).

The subfamily Nomiinae is especially diverse and abundant in Africa, Australia, and Asia (references in Pauly 1990), but it comprises a relatively small portion of the Nearctic halictid fauna. Our 20 species had been placed in four subgenera of the genus *Nomia* (Moure & Hurd 1987). Recently, however, Michener et al. (in press) recognized two genera of North American Nomiinae—*Nomia* = *N. (Acunomia)* + *N. (Curvinomia)*; *Dieunomia* = *N. (Epinomia)* + *N. (Dieunomia)* (see also Cockerell 1910); in this classification *Nomia* is synonymous with *Acunomia* of Pauly (1990).

Among North American species, the nesting biology of the polylectic, solitary, alkali bee, *N. melanderi* Cockerell, is well studied (Johansen et al. 1978), as is another solitary species, *Dieunomia triangulifera* (Vachal), which is a specialist on composites (Rau 1929; Cross & Bohart

1960; unpublished data). There are brief, scattered biological notes on three other species: *D. nevadensis* Cockerell (Kerfoot 1964, Cross & Bohart 1960), *D. heteropoda* (Say) (Parker et al. 1986, Blair 1935, Cross & Bohart 1960, Stephen et al. 1969), and *N. nortoni* Cresson (High 1921).

This paper describes aspects of the nesting biology of *Nomia (Curvinomia) tetrazonata* Cockerell, which is of considerable interest because it provides the first record of large multifemale nests in a North American nomiine bee. Data are also presented on previously unknown aspects of the nesting biology of a very large, solitary, composite specialist, *Dieunomia heteropoda* (Smith). For both species, new rearing records for associations with parasitic bees are given. Nest architectural features and behavior provide useful characters which support the generic distinction between *Nomia* and *Dieunomia*.

Materials and Methods

Nomia tetrazonata tetrazonata. The bees were studied at the Buenos Aires National Wildlife Refuge (BANWR), ≈12 km N of Sasabe, Pima County, Arizona, near the Mexican border. BANWR currently consists of upper elevation grassland, mixed with some *Prosopis glandulosa* Torr. (Leguminosae), *Parkinsonia aculeata* L. (Leguminosae), and *Ferocactus* sp. (Cactaceae);

¹ Current address: Department of Entomology, Cornell University, Ithaca NY 14853-0999.

other plants in bloom when the bees were active were *Polygonum pennsylvanicum* L. (Polygonaceae), *Lepidium thurberi* Woot. (Cruciferae), and *Glinus radiata* (Ruiz & Paavo) (Aizoaceae). Before the 1800s and before the introduction of cattle by European settlers, the area now occupied by BANWR was entirely grassland which frequently burned, was without mesquite trees and cacti, and presumably without persistent patches of bare, open soil. The bee fauna then may have been very different.

Bees nested in an aggregation along the northern edge of Mormon Lake, which is sometimes dry. During this study, Mormon Lake was a mostly grass-filled basin which contained a small amount of water when the bees were first discovered. The water covered an area of ≈ 700 m², and was less than 30 cm deep. This "lake" gradually dried out during the course of this study and was dry during the remainder of the year. The nesting site was first visited on 11 July 1991, and I revisited it every 3–6 d during the remainder of the month. After the bees no longer actively provisioned nests (early August), I visited the site at least once a week until 8 September (total visits, 19). In 1992, I revisited the site and surrounding areas at various times in late June and again in early July and found no evidence of *N. tetrazonata* activity. There were no living stages discovered underground in old nests; Mormon Lake was dry, and none of the pollen plants was in bloom.

When the nesting site was discovered in 1991, cursory nest excavations indicated that nests contained large proportions of nearly mature brood (i.e., older larvae and prepupae). Nests were marked with pieces of numbered flagging tape which were secured to the soil using roofing nails. Adult females from some nests were marked for individual recognition using dots of enamel paints placed on the thorax in unique color combinations. Nests were observed continuously by one or two people throughout the times of the day when most provisioning occurred ($n = 6$ nests over 4 d between 12 and 19 July). The color marks of bees entering or leaving a nest were recorded and, for the former, whether or not they were carrying pollen. As an estimate of provisioning activity late in the day, flying bees were collected by sweep netting over the nesting site, and the numbers of females with and without conspicuous pollen loads were tallied; subsamples of bees without pollen were gently squeezed between thumb and forefinger to ascertain if nectar was present in their crops.

Information on diel emergence from nests was obtained by placing inverted plastic cups over the nest entrances ($n = 8$). The bottoms of the cups were replaced with nylon screen to prevent the bees from overheating. The sex of each bee that emerged into a cup was recorded, then the bee was released. Every 15 min, the ground tem-

perature was taken using a Bailey Bat-12 thermocouple thermometer.

I anticipated that the offspring of bees from the active nests would emerge and actively provision cells, but because of the lack of rain, the mesquite did not bloom in the late summer. To determine if all callow bees emerged and did not remain underground until the following year, on 10 August I placed a 1-m² screened emergence trap over an area where bees had been nesting. The sex of captured bees was determined, and the bees were released. In late September, 2 wk after the last bee had been collected from the trap, the soil beneath the trap was excavated to a depth of ≈ 1 m to look for living stages of bees.

Information on nest architecture and additional estimates of numbers of females per nest were obtained through periodic nest excavations. When all nest residents were presumably in their nests (i.e., either before or after the foraging period), a thin slurry of plaster-of-Paris was injected with pressure into the nest using a 20 cc plastic syringe with an 18 gauge hypodermic needle. The plaster was allowed to harden. Nests were excavated by carefully removing soil with a pocket knife, the position of each cell was recorded on graph paper, and the contents of the cells were described. All residents (adult, callow, and immature bees) from a single nest were preserved in a vial of Kahle's solution. Dimensions of pollen masses and measurements of nest cells were made in the laboratory using a stereomicroscope fitted with an ocular micrometer; fine features of cell architecture were also observed under the microscope. Intact pollen masses were collected from cells ($n = 20$), individually placed in vials, and later weighed in the laboratory and dried. Pollen-laden females returning to the nest were carefully collected by trapping them in cups, then transferring them to vials with 70% ethyl alcohol. Information on pollen counts is presented elsewhere.

Statistical tests were calculated using Systat, and are indicated in the text. Unless stated otherwise, results are presented as arithmetic means \pm standard errors.

Dieunomia heteropoda kirbii Smith. *Dieunomia heteropoda* was studied in aggregations along the sides of unpaved roads near Turkey Creek, ≈ 17 km S of the junction of Highways 181 and 186, and 6 km E of Highway 181 near the western edge of Coronado National Forest (Cochise County). Most observations came from a site near the SunGlow Mission Ranch, which is ≈ 1 km east of the Cottonwood Canyon entrance to Coronado National Forest. Information on the provisioning behavior of this species was obtained using the same methods as for *N. tetrazonata*.

Voucher Specimens. Adult specimens with voucher labels of *Nomia tetrazonata*, its nest cells, and its associated parasites, are deposited

in the Cornell University Insect Collection, Ithaca, NY (lot 1216); undescribed immature stages of *N. tetrazonata* are deposited in the American Museum of Natural History, New York. Vouchers of *Dieunomia heteropoda* and its associated parasite are in the Cornell University Collection (lot 1216). Additional vouchers of the bee species are in the University of Arizona Insect Collection, Tucson, and the Snow Entomological Museum, University of Kansas, Lawrence.

Results

Nomia tetrazonata. *Nest Sites and Seasonal Activity*. The bees nested in an arc around what would have been the northwest shore of Mormon Lake. The nest aggregation occupied an area ≈ 10 by 140 m, but nests were not evenly distributed throughout this area. The density of nests ranged from 1 to 14 nests per m^2 , but a systematic study of the spatial distribution of nests was not made. Soil samples from the nesting site are available from the author.

When the bees were first discovered, they presumably were active for at least several weeks because nests already contained numerous cells with pollen masses with eggs as well as various larval stages (including prepupae). There were no pupae or callow adults. Collection records also suggest these bees become active at least as early as late June. I collected males in northern Pima County (vicinity of Tucson) as early as mid-April in 1992; specimens in the University of Arizona Insect Collection were also collected as early as April in southern Pima County. Throughout its range (southwestern United States to Sonora and Baja California in México), dates of collection range from 25 March to 28 October (Ribble 1965).

Bees at BANWR actively provisioned nests with pollen and nectar from 12 July until the end of the month. On 24 July, very few bees entered nests with pollen and by 29 July, all pollen provisioning had ceased. Whether this cessation of provisioning activity relates to life history characteristics or to the lack of pollen because of a draught is unknown.

Nests excavated at this time (24 July–1 August) contained young and mature larvae, many pupae and callow adults, and worn (presumably old) females. The brood from these nests began to emerge in mid-July, based on the first date that males were seen flying. Males were first noticed flying on 16 July and became abundant by 21 July; the last newly emerged male was collected from an emergence trap on 22 August. Males were occasionally collected flying near vegetation through 11 September.

After emerging from natal nests, males flew over the nesting site and pounced on females, sometimes on other *Nomia* males and also on males of a parasitic bee, *Triepeolus verbesinae*

(Cockerell). Mating behavior is being described elsewhere (unpublished data). Males spent the night on vegetation and could be collected in large numbers very early in the morning, although they were not in sleeping clusters like those of many other aculeate Hymenoptera.

Unworn female bees were first noticed on 21 July and continued to emerge in increasing numbers throughout early August. Between 17 and 22 August, few females were emerging; no females emerged between 22 August and 1 September and two females emerged between 1 and 8 September, after which no more females emerged. These August and September females did not provision nests in the area. Because of the lack of seasonal rains in July and August, mesquite did not bloom in late summer, which presumably shortened the pollen-gathering season. These newly emerged females also did not return to their natal nests to enter diapause: excavations of numerous plots where bees had been nesting failed to reveal any evidence of living stages of bees. Likewise, all bees that became adults left the natal nests as shown by the lack of living bees in the area under an emergence trap.

Several other small populations of this species were discovered but for various reasons could not be studied in any detail. Although anecdotal, the following observations suggest that multifemale nests are not unusual for this species, and they might suggest that *N. tetrazonata* does not have aggregations that persist over several seasons as do those of some other nomiines (e.g., *N. melanderi*, *D. triangulifera*). A very small aggregation of *N. tetrazonata* was found on 27 July 1991 nesting in the bed of a dried stock tank at the University of Arizona Oracle Farms (≈ 14 km SW of Oracle, Pinal Co., AZ); the nest entrances were in the deep cracks of the soil, so it was impractical to excavate nests, but observations of many bees carrying pollen into the same place in a crack indicate that these bees may also have been communal. The following year there was no sign of these bees in this area (the stock tank contained some water at least through mid-July, but other halictids were nesting around its edge). Another very small aggregation of 14 nests was in a patch (1 \times 2 m) of a watered garden in a residential area in east Tucson, AZ (Pima County) on 12 August 1991. Several females carried pollen into each of at least five nests, and then exited the nests without pollen. The owners had lived at this residence for 4 yr and never noticed bees in their garden previously (and their panic associated with an allergy to bee venom suggested they would have noticed nesting bees if an aggregation had been present earlier). Another resident of a home in northwest Tucson had bees nesting in the soil among landscaped rocks surrounding her swimming pool (25 June 1992). Again, the owner wished to eliminate the bees,

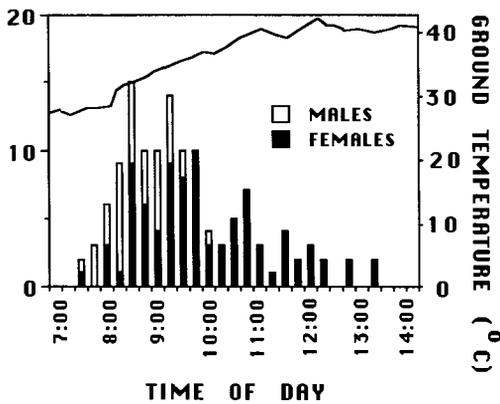


Fig. 1. Diel emergence of male and female *Nomia tetrazonata* from the nests in relation to ground temperature.

but brief observations indicated that several females were carrying pollen into the same nest. The owner informed me that "the bees just suddenly appeared" and that she had lived in the house for more than 10 yr and never before had bees. No males were seen flying, and all females ($n = 7$) had sperm in their spermathecae.

Diel Activity and Nest Provisioning Behavior. As usual with bees, males became active earlier in the day than females. Males spent the night on vegetation and began flying between 0700 and 0800 hours (MST), or earlier if the temperature rose above $\approx 24^{\circ}\text{C}$. The emergence from nests of newly eclosed adult males peaked between 0800 and 0830 hours, and no newly emerged males were recorded after 1030 hours (Fig. 1). A few females became active as early as males but most began emerging later. The distribution of female emergence was broader; a few females first emerged as late as 1315 hours.

Most pollen collecting took place before 1400 hours, but many females continued to fly until 1730 or 1800 hours. Sweep samples of these bees made between 1600 and 1700 hours showed that most bees were not collecting pollen (5 of 112 females had conspicuous pollen loads), but probably all were gathering nectar (15 of 15 bees regurgitated nectar when they were gently squeezed).

Some nests had many females, so it was often difficult to identify reliably the marks of incoming bees without capturing them (which was typically not done). Often there was a jumble of bees jostling at the nest entrance to enter with their pollen loads. Consequently, the following data on provisioning behavior are only approximations because most observations did not cover the entire period of foraging, and the high levels of activity at nest entrances made it difficult to ascertain the identity of returning bees; data are based on the smaller sample of bees that were positively identified. Provisioning trips of indi-

vidually marked bees (data collected on 14 and 21 July) lasted from 7 to 40 min (mean, 21.9 ± 2.53 min [mean \pm SE], $n = 15$), and between trips the bees remained within the nest for 3–38 min (mean, 12.9 ± 2.45 min, $n = 15$). At least 12 females made four provisioning trips in a day; 4 females made at least six trips in one day, and 1 female made seven trips. Pollen grains from cells were identified as those of *Prosopis*, *Polygonum pennsylvanicum*, *Lepidium thurberi*, and *Glinus radiata*.

Group Living Behavior and Nest Architecture. Nest entrances were not guarded, and bees readily departed from and entered nests. Estimates of the numbers of active females using a nest varied, depending on the method used. On 14 and 16 July, before nests contained many newly eclosed adults (five rapidly excavated nests did not contain brood older than white-eyed pupae), females were captured and marked as they exited nests in the morning. The mean number of consecutively exiting females per nest was 16.1 ± 3.99 (harmonic mean, 12.07, $n = 7$). Forty-seven female bees were captured and marked as they exited one nest on 2 d; of these, at least 14 marked bees entered the nest carrying pollen, as did 6 consecutive unmarked bees. Therefore, at least 20 bees actively provisioned cells in this nest, based on a conservative estimate. On 21 July, cups were placed over nest entrances, and the females that emerged from each nest were captured and preserved (three excavated nests at this time had many male and female pupae with black eyes, and some callow males, but only two callow females). This method yielded a mean estimate of 12.3 ± 5.86 females per nest (harmonic mean, 1.9, $n = 6$) (excluding three females with unworn wings from one nest and one unworn female from another). At this time, three nests each had only one unworn female, with only 1, 2, and 4 new cells. Some nests were filled with plaster-of-Paris either early in the morning or late in the day, then excavated (between 14 and 29 July), which gave an estimate of 11.1 ± 1.64 female residents per nest (harmonic mean, 8.33, $n = 9$). For these nine nests, if unworn females are excluded, the mean number of females per nest (10.1 ± 1.56) is slightly lower. Excavated nests contained at least several empty cells as well as at least several cells only partially filled with pollen.

A sample of three to seven females was dissected from each of five nests to determine associations between body size, body wear, ovarian development, and mating status (females collected between 12 and 24 July). In all cases, females with well-worn wings and mandibles had either well-developed ovarioles or more slender ones but with yellow bodies, pollen in their guts, and all had sperm in their spermathecae. A sample of five females with unworn

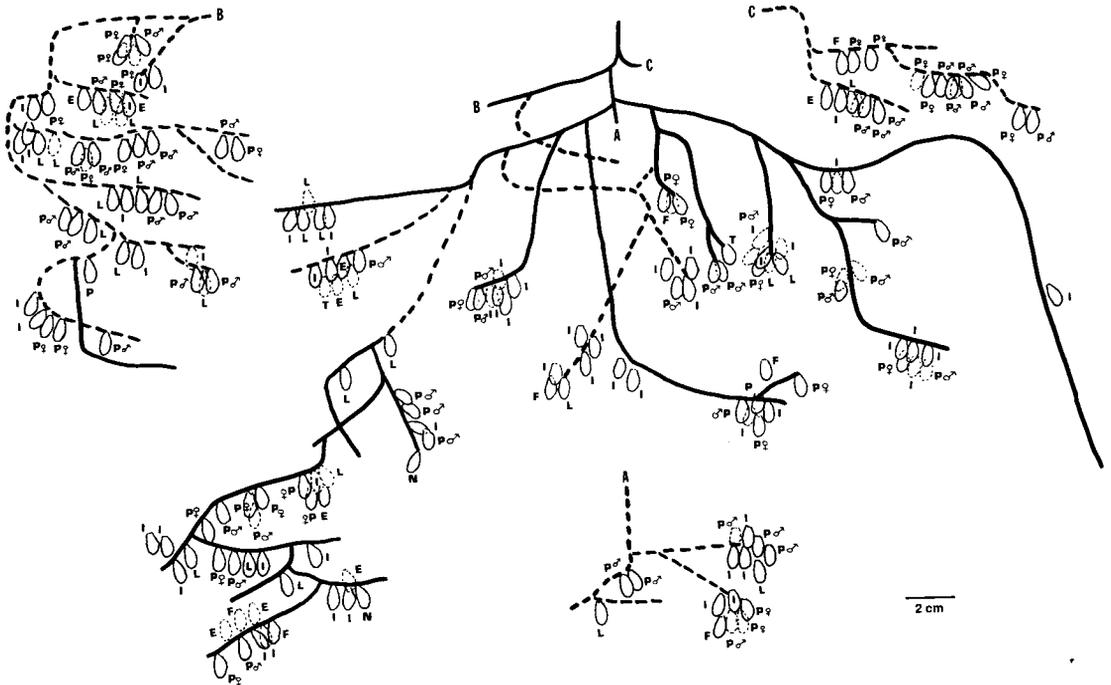


Fig. 2. Schematic diagram of a mature nest of *Nomia tetrazonata* from Arizona. This nest was occupied by 8 adult females and 1 adult males when it was excavated on 24 July 1991. The dashed lines (---) indicate nest structures which are going away from the viewer. A, B, and C are portions of the nest which connect to corresponding letters on the main illustration, but have been separated to facilitate presentation. Symbols describing cell contents: N = empty, open cell; E = pollen mass with egg; L = larva with some pollen; I = post-defecating larvae (prepupa); P = pupa (sex indicated by symbol); T = *Triepeolus verbesinae* prepupa; and F = fungus/mold. Scale bar = 2 cm. Tunnel lengths are drawn to scale, but the diameter of the tunnel is not (see text).

wings was also dissected from one nest (collected 26 July). These females also had well-developed ovarioles, pollen in their guts, and were mated, possibly suggesting that newly emerged females return to their natal nests. Two callow females with milky wings had slender ovaries and were not mated, suggesting that females leave the nest to mate.

A representative mature nest of *N. tetrazonata*, collected with eight adult females and 1 adult male, is shown in Fig. 2. Each nest entrance was a smoothed circular hole with a slight constriction at the entrance (mean diameter, 4.53 mm, $s = 0.14$, $n = 10$). The entrance lacked a turret as seen in some other Nominae (see Cross & Bohart 1960), and neither the entrance nor the tunnel were obviously coated with chemical secretions. Most nests did not have any accumulated mounds of soil (tumuli) around the entrances, probably because the high winds dispersed the excavated soil. Below the entrance the tunnel diameter was slightly larger (mean, 5.99, $s = 0.19$, $n = 10$). Tunnels usually went straight into the soil for several centimeters, then branched repeatedly in varying compass directions. Each branch meandered downward in var-

ious directions from the entrance, and itself branched.

Based on carefully excavated nests which were filled with plaster-of-Paris, the number of cells per nest varied from 23 to 191 (mean, 94.2 ± 15.8 , $n = 9$). Excluding unworn bees, there is a weak but nonsignificant association between the number of females in a nest and the total number of cells (Pearson's $r = 0.49$, $P = 0.183$, $n = 9$). Nests were carefully excavated only toward the end of the active season, so it is not possible to meaningfully correlate the numbers of new cells and resident bees to determine if bees cooperatively provision cells.

Cells were found from a depth of ≈ 4 –30 cm; sometimes they were isolated but were usually found clumped together with up to 10 other cells. Cells were attached directly to tunnels or with lateral tunnels shorter than one cell length.

The long axis of a cell was often perpendicular to the soil surface, as with other *Nomia*, although sometimes cell orientation varied from a slight deviation from vertical to nearly parallel to the soil surface. Each cell was generally oval in shape, not flattened on one side, and the walls were obviously coated with hydrophobic chem-

ical secretions (cell dimensions, $n = 8$ [mean \pm s]: length, 9.93 ± 0.7 mm; width at the widest part, 5.52 ± 0.4 mm; entrance diameter, 3.7 ± 0.27 mm). Cells were closed with a short plug of soil (3.28 ± 1.15 mm), the inner side of which had a spiral impression which was coated with secretions, except for a small part at the center. In general structure, the cell did not differ from those illustrated for *Nomia melanderi* (Stephen et al. 1969) or *Pseudapis diversipes* (Latreille) (Rozen 1986); *Pseudapis* is sometimes considered a subgenus of *Nomia*. In lateral view the pollen masses were slightly flattened on top, more rounded on the bottom, and circular when viewed from above; each mass was ≈ 3 mm high with a diameter of ≈ 5.5 mm. Pollen masses sat on the bottom of cells; eggs were placed on top of the mass and were not obviously coated with chemical secretions, as occurs in an Australian *Nomia* (*Austronomia*) sp. (personal observation). The pollen mass was usually not set slightly on edge at an angle, as illustrated for *N. melanderi* (Stephen et al. 1969) or *P. diversipes* (Rozen 1986), although some pollen masses were slightly tilted. Larval feces were defecated in the cells and were deposited as flat bands extending from the floor of the cell to more than one-third up the cell wall.

Natural Enemies. The potential natural enemies observed flying at this site were the parasitic bee *Triepeolus verbessinae* (Cockerell) (Nomadinae), of which the males were remarkably abundant, and the bee fly *Heterostylum* sp. (Diptera: Bombyliidae). Four specimens of the bombyliid were recovered from the emergence trap, but none was obtained during nest excavations to definitely confirm the association. Five *T. verbessinae* prepupae were recovered from nest excavations; two of these were reared to the adult stage, providing the first confirmed host record for this species. Based on excavations, the success rate of parasitism was quite low ($\approx 2\%$ of 285 cells).

***Dieunomia heteropoda*.** *Nesting Site and Seasonal Activity.* *Dieunomia heteropoda* is an abundant bee in the Turkey Creek area. Nests were easily located because the entrances were surrounded by large mounds (tumuli) of excavated soil. Most nests were in one of six aggregations along the sides of unpaved roads, although occasionally nests were isolated from others by ≈ 100 m. At the SunGlow site there were approximately 180 nests in an area 2 by 30 m. Nests were loosely aggregated and reached densities of up to 12 nests per m^2 . The area had extensive stands of flowering *Helianthus petiolaris* Nutt. (Asteraceae), which females visited for both pollen and nectar. Males visited these plants for nectar and pounced on foraging females; males also spent nights on the open capitula, with 3.0 ± 1.78 [s] males per capitulum

(excluding the majority of the capitula which had no bees) (range, 1–7, $n = 13$).

The sites were first visited on 12 August 1991 and showed no signs of any bee activity; most of the sunflowers were not yet in bloom. On 18 August, flowers had begun to bloom, and there were many males flying from 5 to ≈ 15 cm over the surface, attempting to mate with females. The mating biology of this species is being described elsewhere (unpublished data). A few females were nesting, but none entered nests with more than trace amounts of pollen. From this date until the end of August, males were abundant at the emergence-nesting areas and on nearby sunflowers. After this time they became increasingly scarce and were effectively absent from the site by the middle of September (one male was observed flying on 21 September). Females, in contrast, became increasingly abundant and were actively provisioning nests until the end of September and the first days of October. No bees were active when the sites were visited on 7 October.

Diel Activity and Provisioning Behavior. Females began provisioning nests at ≈ 0730 hours, or when the ground temperature rose above $\approx 20^\circ\text{C}$, and provisioned throughout the day until ≈ 1400 hours. The sunflowers produced a late-afternoon (1600–1700 hours) pulse of pollen, as known for *Helianthus annuus* (Neff & Simpson 1990). Female *D. heteropoda*, however, did not collect pollen during the late afternoon, although bumble bees (*Bombus*) continued collecting.

At all the sites, sunflowers were abundant and presumably bees did not have to fly far to gather pollen. Each plant had from 4 to 126 capitula offering pollen (40.6 ± 4.58 , $n = 45$ plants), and bees spent an average time of 8.3 ± 0.91 s per flower head ($n = 37$ visits by eight bees). Females made up to seven foraging trips per day (4.47 ± 0.28 per female, $n = 19$). This value was calculated excluding females for which only a single trip was recorded because singletons probably relate to missing observations rather than bee behavior. Provisioning trips lasted 42.15 ± 3.68 min (range, 8–183 min; $n = 76$), and between trips females remained within their nests for 12.02 ± 1.99 min (range, 4 to 143 min; $n = 76$). In general, provisioning trips were of longer duration as the day progressed. At the extremes, the mean duration for a female's first trip of the day was 28.65 ± 2.31 min ($n = 22$), and was significantly faster than her last trip of the day (65 ± 10.03 min, $n = 22$) ($t = -3.683$, $df = 22$, $P = 0.001$ (paired t -test)).

Nearly all females were solitary nesters, but in each of two cases two females were known to provision actively in the same nest for at least 2 d.

Nest Architecture. Nests of *D. heteropoda* from the Turkey Creek area consisted of long, more or less vertical tunnels, with lateral tunnels

perpendicular to the main shaft. Cells hung vertically from these laterals and occurred at depths of 30–70 cm. Other than differences in cell depth, nest architectural features of Turkey Creek *D. heteropoda* did not differ in significant ways from nests from Utah described by Parker et al. (1986), or a nest from Kansas by Cross & Bohart (1960). Cells and pollen masses were of the same shape and form as those illustrated by Stephen et al. (1969).

Natural Enemies. A parasitic bee, *Tripeolus distinctus* (Cresson) (Nomadinae), was frequently observed flying low over the nesting sites, and sometimes females were observed entering *D. heteropoda* nests, where they remained for 168.3 s (range, 45–300; $s = 127.7$, $n = 5$); brief entries for less than 10 s were not counted because they probably represented nest inspection rather than oviposition. Three *Tripeolus* prepupae and a pupa were recovered during nest excavations but were not reared to the adult stage successfully. No other *Tripeolus* were observed in the area. *T. distinctus* has also been reared from nests of *Dieunomia triangulifera* in Kansas (personal observation).

Discussion

Among bees, facultative or obligate communal behavior is known in every major lineage, including Colletidae (Sakagami & Zucchi 1978), Andrenidae (Rozen 1989, Danforth 1991), Halictidae (references in Michener 1990a, and herein), Megachilidae (Garófalo et al. 1992), and Anthophoridae + Apidae (Zucchi et al. 1969; Rozen 1984; also references in Michener 1990b). Ecologically, such behavior occurs in nearly all kinds of habitats, from tropical to xeric areas. Results of this study provide the first documentation of communal behavior in a Nearctic nomiine bee, although multifemale groups of presumably independent females have been reported in nests of various Old World Nomiinae, including *N. (Austromonia) australica* Smith (Rayment 1956), *N. (Austromonia) sp.* (Kukuk 1990), *N. (Hoplonomia) punctulata* Dalla Torre (Masuda 1943, cited in Hirashima 1961), *N. (Afronomia) sjostedti* (Friese) (= *N. hypochrysea* Cockerell) (Michener 1969), *N. (Leuconomia) candida* Smith (Michener 1969), *N. (Pseudapis) diversipes* (Rozen 1986), and some nests of *N. (Rhopalomelissa) sp.* (Michener, 1969). Batra (1966) observed that each of several nests of both *N. capitata* Smith, and *N. (Pseudapis) oxybeloides* Smith contained 1–12 females. In *N. capitata* and *N. (P.) oxybeloides*, most females were inseminated with developed ovaries (the exceptions were unworn, presumably newly emerged bees) as with *N. tetrazonata*. These brief reports indicate that the pearly-banded *Nomia* and their relatives deserve far more study.

Each well-worn female in a *N. tetrazonata* nest was mated with developed ovaries, as were females collected when they were gathering pollen, indicating that most or all the females are reproductively active. None of the marked females switched nests and provisioned in nests other than the ones from which they were first collected, unlike another communal halictine bee (Abrams & Eickwort 1980). There were no obvious signs of agonistic interactions among nest-mates at nest entrances, and Kukuk (1990) showed that females of a communal *N. (Austromonia) sp.* are less aggressive toward nest-mates than unfamiliar females.

Evans & Hook (1986), among others, have hypothesized that nesting in very dry and compact soil might favor females that nest communally because of the effort saved from not having to excavate a main tunnel through the hardened surface. No attempt was made to quantify soil hardness in this study, but my impression was that the soil was much less difficult to dig than various halictine and nomiine nests I have excavated. Another hypothesized benefit from communal nesting is improved efficacy of defense against natural enemies (e.g., Wcislo et al. 1988). Rates of parasitism in excavated nests were low, but there is insufficient information to compare rates in populous nests versus nests occupied by few bees. Nomiine bees are not the usual hosts for *Tripeolus* cuckoos. These parasites are usually associated with hosts in the Anthophorinae, although one species is associated with Oxaeidae and a few with Nomiinae (Krombein et al. 1979; Results); the two *Tripeolus* species from this study which parasitize nomiines are probably not closely related (*A. Roig-Alsina, in litt.*).

In contrast to *N. tetrazonata*, the pollen specialist *D. heteropoda* is solitary, although a few observations suggest that some females might occupy a nest dug by another bee. Moure & Hurd (1987, p. 40) give a misinterpretation in stating that *D. heteropoda* females are known to nest "in abandoned burrows of *Tachysphex mundus* [Sphecidae]." The reverse is true; the wasp sometimes nests in abandoned burrows of the bee (Kurczewski 1979).

Certain features of the nesting biology of nomiine bees may provide useful systematic characters (for a partial review of nomiine nest architecture, see Iwata 1976: pp. 346ff.). The nest architecture of *D. heteropoda* agrees with that of nests studied in Utah (Parker et al. 1986) and Kansas (see Cross & Bohart 1960), except for differences in nest depth, which may relate to varying edaphic conditions. Other features such as shape of pollen mass, patterns of fecal deposits, and nest structure (e.g., presence of horizontal turrets; cells in rows along a lateral tunnel which is perpendicular to the main tunnel) also agree with published studies of this species. The nest features of *D. heteropoda* are very similar to

those of *D. triangulifera* and *D. nevadensis* (Cross & Bohart 1960, Kerfoot 1964) and differ from *N. tetrazonata* and other pearly-banded *Nomia* and their relatives. Nests of *N. tetrazonata* differ from those of *Dieunomia* in lacking nest turrets and long lateral tunnels. Instead, they have a tendency to cluster cells loosely. These tendencies produce nest structures more similar to those of *N. melanderi* (Stephen et al. 1969) or Old World species illustrated by Batra (1966), Michener (1964, 1969), and that of *N. (Austronomia) australica* (Rayment 1956). There is no evidence of a cavity surrounding cell clusters in *N. tetrazonata* nests, as described for *N. nortoni* by High (1921) (although Parks [1928] does not mention such a cavity) or some Old World nomiines (see Hirashima 1961). The slightly flattened but circular pollen mass of *N. tetrazonata* differs considerably from those of *Dieunomia* in overall shape, but it is similar in shape to that of *N. melanderi* (Stephen et al. 1969) or *P. diversipes* (Rozen 1986).

The pollen-gathering preferences of *Dieunomia* and North American *Nomia* may differ as well, based on the limited information available. *Nomia* are broadly polylectic. *N. tetrazonata*, for example, used pollen from at least four species of plants during this study, and this species has been collected on 54 plant species from 48 genera in 21 families (Ribble 1965). Most *Dieunomia*, in contrast, are composite specialists and often are associated with Helianthini. *D. nevadensis* is apparently exceptional, and Hurd et al. (1980) reported that several subspecies of *D. nevadensis* visit sunflowers (*Helianthus*) only for nectar. Although *D. nevadensis* has been considered a polylege because it has been collected from numerous plants (Moure & Hurd 1987), it probably visits most of them only to drink nectar.

Behavioral characters support the decision by Michener et al. (in press) to recognize *Dieunomia* at the generic level. *Dieunomia* differ from other nomiines in having (1) horizontal nest turrets (some *Rhopalomesa* and *Austronomia* have vertical turrets, whereas other nomiines lack them); (2) modified ovoid-shaped pollen masses (other nomiines have rectangular or flattened spherical pollen masses); and (3) rows of nest cells hung vertically from long laterals perpendicular to the main tunnel (other nomiines either have cells loosely clustered, within cavities, or at the ends of individual branches of the tunnel).

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References Cited

- Abrams, J. & G. C. Eickwort. 1980. Biology of the communal sweat bee *Agapostemon virescens* (Hymenoptera: Halictidae) in New York state. Search (Corn. Univ. Agric. Exp. Stn.), no. 1.
- Batra, S.W.T. 1966. Social behavior and nests of some nomiine bees in India (Hymenoptera, Halictidae). *Insectes Soc.* 13: 145-154.
- Blair, B. H. 1935. The bees of the group *Dieunomia*. *J. N.Y. Entomol. Soc.* 43: 201-214.
- Cockerell, T.D.A. 1910. The North American bees of the genus *Nomia*. *Proc. U.S. Natl. Mus.* 38: 289-298.
- Cross, E. A. & G. E. Bohart. 1960. The biology of *Nomia (Epinomia) triangulifera* with comparative notes on other species of *Nomia*. *Univ. Kans. Sci. Bull.* 41: 761-792.
- Danforth, B. N. 1991. Female foraging and intranest behavior of a communal bee, *Perdita portalis* (Hymenoptera: Andrenidae). *Ann. Entomol. Soc. Am.* 84: 537-548.
- Evans, H. E. & A. W. Hook. 1986. Nesting behavior of Australian *Cerceris* digger wasps, with special reference to nest re-utilization and nest sharing (Hymenoptera, Sphecidae). *Sociobiology* 11: 275-302.
- Garófalo, C. A., F. Camillo, M.J.O. Campos & J. C. Serrano. 1992. Nest re-use and communal nesting in *Microthurga corumbae* (Hymenoptera, Megachilidae), with special reference to nest defense. *Insectes Soc.* 39: 301-311.
- High, M. M. 1921. An unusual type of injury to sweet potatoes in Texas by a burrowing bee. *J. Econ. Entomol.* 14: 306-307.
- Hirashima, Y. 1961. Monographic study of the subfamily Nomiinae of Japan (Hymenoptera, Apoidea). *Acta Hymenopt.* 1: 241-303.
- Hurd, P. D. Jr., W. E. LaBerge & E. G. Linsley. 1980. Principal sunflower bees of North America with em-

- phasis on the southwestern United States. *Smithsonian Contrib. Zool.* 310: 1–158.
- Iwata, K.** 1976. Evolution of instinct (transl. 1971, from Japanese). Amerind, New Delhi.
- Johansen, C. A., D. F. Mayer & J. D. Eves.** 1978. Biology and management of the alkali bee, *Nomia melanderi* Cockerell (Hymenoptera: Halictidae). *Melanderia* 28: 25–33.
- Kerfoot, W. B.** 1964. Observations on the nests of *Nomia nevadensis bakeri* with comparative notes on *Nomia nevadensis arizonensis*. *J. Kans. Entomol. Soc.* 37: 152–157.
- Krombein, K. V., P. D. Hurd, Jr., D. R. Smith & B. D. Burks.** 1979. Catalog of Hymenoptera in America north of Mexico. Smithsonian Institution Press, Washington D.C.
- Kukuk, P. F.** 1990. Nest-mate recognition in a group-living nomiine bee (Hymenoptera, Nomiinae), pp. 509–510. In G. K. Veeresh, B. Mallik & C. A. Viraktamath [eds], Social insects and the environment [Proc. 11th Internatl. Congr. IUSSI]. Oxford & IBH Publ. Co, New Delhi.
- Kurczewski, F. E.** 1979. Nesting behavior of *Tachysphex mundus* Fox (Hymenoptera, Sphecidae, Larrinae). *Pol. Pismo Entomol.* 49: 641–647.
- Masuda, H.** 1943. Biological notes on *Nomia punctata* Westwood (Hym., Andrenidae). *Mushi* 15: 16–27 (in Japanese).
- Michener, C. D.** 1964. Nests of *Nomia pulchribalteata*. *J. Kans. Entomol. Soc.* 37: 116–118.
1969. Notes on the nests and life histories of some African halictid bees with description of a new species. *Trans. Am. Entomol. Soc.* 94: 473–497.
- 1990a. Reproduction and castes in social halictine bees, pp. 77–122. In W. Engels [ed.], *Social insects*. Springer, New York.
- 1990b. Castes in xylocopine bees, pp. 123–146. In W. Engels [ed.], *Social insects*. Springer, New York.
- Michener, C. D., R. J. McGinley & B. N. Danforth.** (IN PRESS). *Bee Genera of North and Central America*. Smithsonian Institution Press, Washington D.C.
- Moure, J. C., CMF & P. D. Hurd, Jr.** 1987. An annotated catalog of the halictid bees of the western hemisphere (Hymenoptera: Halictidae). Smithsonian Institution Press, Washington D.C.
- Neff, J. L. & B. B. Simpson.** 1990. The roles of phenology and reward structure in the pollination biology of wild sunflower (*Helianthus annuus* L., Asteraceae). *Isr. J. Bot.* 39: 197–216.
- Parker, F. D., T. L. Griswold & J. H. Botsford.** 1986. Biological notes on *Nomia heteropoda* Say (Hymenoptera: Halictidae). *Pan.-Pac. Entomol.* 62: 91–94.
- Parks, H. B.** 1928. Nesting habits of the bees, *Nomia* [sic] *nortonii* Cresson, in Texas. *Bull. Brooklyn Entomol. Soc.* 23:263.
- Pauly, A.** 1990. Classification des Nomiinae Africains. *Ann. Sci. Zool.* 261: 1–206.
- Rau, P.** 1929. The nesting habits of the burrowing bee, *Epinomia triangulifera*. *Psyche* 36: 243–248.
- Rayment, T.** 1956. The *Nomia australica* Sm. complex— its taxonomy, morphology and biology with the description of a new mutillid wasp. *Aust. Zool.* 12:176–200.
- Ribble, D. W.** 1965. A revision of the banded subgenera of *Nomia* in America (Hymenoptera: Halictidae). *Univ. Kans. Sci. Bull.* 45: 277–359.
- Rozen, J. G., Jr.** 1984. Comparative nesting biology of the bee tribe Exomalopsini (Apoidea, Anthophoridae). *Am. Mus. Novit.* 2798: 1–37.
1986. The natural history of the Old World nomadine parasitic bee *Pasites maculatus* (Anthophoridae: Nomadinae) and its host *Pseudapis diversipes* (Halictidae: Nomiinae). *Am. Mus. Novit.* 2861: 1–8.
1989. Life history studies of the “primitive” panurgine bees (Hymenoptera: Andrenidae: Panurginae). *Am. Mus. Novit.* 2962: 1–27.
- Sakagami, S. F. & R. Zucchi.** 1978. Nests of *Hylaeus* (*Hylaeopsis*) *tricolor*: the first record of non-solitary life in colletid bees, with notes on communal and quasisocial colonies. *J. Kans. Entomol. Soc.* 51: 597–614.
- Stephen, W. P., G. E. Bohart & P. F. Torchio.** 1969. The biology and external morphology of bees. *Publ. Agric. Exp. Station, Oregon State Univ.* 140 pp.
- Wcislo, W. T., M. J. West-Eberhard & W. G. Eberhard.** 1988. Natural history and behavior of a primitively social wasp, *Auplopus semialatus*. and its parasite, *Irenangelus eberhardi* (Hymenoptera: Pompilidae). *J. Insect Behav.* 1: 247–260.
- Zucchi, R., S. F. Sakagami & J. M. F. de Camargo.** 1969. Biological observations on a neotropical parasocial bee, *Eulaema nigrita*, with a review of the biology of Euglossinae (Hymenoptera, Apidae). A comparative study. *J. Fac. Sci. Hokkaido Univ. Ser. VI (Zoology)* 17: 271–380.

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