

Mating behaviour in the bees, *Dieunomia heteropoda* and *Nomia tetrazonata*, with a review of courtship in Nomiinae (Hymenoptera: Halictidae)

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Males of many bees in the subfamily Nomiinae (Halictidae) have numerous secondary sexual characters, which provide much systematic information. Similarly, the use of these structures by males during sexual behaviour may provide useful characters, but the courtship and copulatory behaviour of most of these bees is not known. Structures and behaviour used for courtship and mating are described for two species of nomiine bees, *Dieunomia heteropoda* and *Nomia tetrazonata*, along with brief observations of mating in a parasitic bee, *Triepeolus verbesinae* (Apidae: Nomadinae). A review of mating behaviour within the Nomiinae shows no obvious phyletic patterns, based upon present limited knowledge. The species-specific nature of the male secondary sexual characters suggests they may have evolved in the context of sexual selection, but behavioural data from populations of additional species are needed to evaluate the hypothesis adequately.

KEYWORDS: mating behaviour; sexual selection; morphology; evolution.

Introduction

Bees in the family Halictidae are an excellent group to study how an organism's behaviour partially creates its selective environment (Wcislo, 1989; Lewontin, 1991). Among species placed in the Halictinae there is effectively no precopulatory courtship behaviour; copulatory courtship is apparently rare, although few studies have looked explicitly for pertinent evidence (see references in Wcislo *et al.*, 1992). Halictine males typically have few structural secondary sex characters, other than elongate antennae (for exceptions see Roberts, 1972). The sister taxon to Halictinae is Nomiinae, of which the males, by contrast, are richly endowed with secondary sexual characters (e.g. illustrations in Cross, 1958; Ribble, 1965; Pauly, 1990; Results).

Nomiine bees are extremely diverse and abundant in Asia, Australia and Africa, but there are only 20 North American species, presently placed in two genera (Cockerell, 1910; Michener *et al.*, 1994; but see Pauly, 1990). There has been a detailed study of one New World species (Wcislo *et al.*, 1992), along with brief observations for several

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other species (Table 1). We describe here the mating behaviour of two species of nomiine bees, *Dieunomia heteropoda* (Smith) and *Nomia tetrazonata* (Cockerell), and summarize data on mating behaviour of nomiine bees. We also provide notes describing the mating behaviour of a parasitic bee, *Triepeolus verbesinae* (Ckll). (Hymenoptera: Nomadinae). The Discussion considers the correspondence between secondary sexual structural characters and their use during mating behaviour, and the implications of this correspondence for understanding behavioural and morphological evolution.

Materials and methods

Dieunomia heteropoda

The mating behaviour of *Dieunomia heteropoda* was studied at aggregations of nests along the sides of unpaved roads near Turkey Creek, approximately 17 km south of the junction of Arizona Highways 181 and 186, and 6 km east of AZ Highway 181, near the western edge of Coronado National Forest (Cochise Co., AZ) (for a more detailed description of the site see Weislo, 1993).

Bees were observed between mid-August and September 1991. Matings were recorded with a hand-held (or rarely, tripod-mounted) Panasonic 8 mm video camera fitted with a macrolens. In some cases simultaneous audio recordings were made with an optical transducer, which transduced cuticular vibrations into sound, which were then recorded using a Sony Model TCM-5000EV cassette tape-recorder (techniques and equipment from Spangler, 1991). These recordings were analysed by playing them through a Krohn-Hite filter (model 3550) to a Kay Elemetrics DSP Sonagraph (model 5500).

Some males were marked with individual colour marks of enamel paint (Testors), but most were not. Males were collected on flowers, patrolling over the nesting/emergence site, or while mating with females; they were then placed in individual vials, kept cool and brought back to the laboratory where they were weighed, and then frozen.

Nomia tetrazonata

The mating behaviour of *Nomia tetrazonata* was briefly studied at an aggregation of these bees at the Buenos Aires National Wildlife Refuge (BANWR), approximately 12 km north of Sasabe (Pima Co.), Arizona, near the Mexican border (for details see Weislo, 1993). Matings were infrequently observed, so it was impossible to obtain quantitative information using audio or video recordings, and information is based upon visual observations in the field.

Nomia tetrazonata were observed in July and August 1991, although records from labels on specimens in the University of Arizona Insect Collection suggest that these bees become active much earlier in the year. Males were collected in northern Pima Co. (Tucson vicinity) as early as mid-April (1992); throughout its range (southwestern USA to Sonora and Baja California in México), dates of collection range from 25 March to 28 October (Ribble, 1965).

Data are presented as arithmetic mean \pm SE, unless indicated otherwise. Statistical analyses are indicated in the text and were performed using the SYSTAT package.

Structural features. Morphological features were studied from scanning electron micrographs taken of gold-plated specimens using a Jeol electron microscope, at electron voltages and magnifications indicated in the figures.

Table 1. Summary of information on mating behaviour of nomiine bees. The behaviour performed by the male, and directed toward the female (F) is described.

Species	Legs I	Legs II	Metasoma	Thoracic structures		Antennae		Duration (mean ± SD, seconds)		Location of males ^a	Reference
				Precopulation	Copulation	Precopulation	Copulation	Precopulation	Copulation		
<i>Dieunomia triangulifera</i> (Kansas)	Tap F prothorax; stroke F; pleura	Stroke F pleura	Drums F metasoma	Rhythmic buzzing (~ 600 Hz)	Rhythmic buzzing (~ 1200 Hz)	Moved slowly down; rapidly up	No movement	70 ± 27	10 ± 4	E, f	Weislo <i>et al.</i> (1992)
<i>Dieunomia triangulifera</i>	Not mentioned	Not mentioned	Drums F metasoma	Not mentioned	Not mentioned	Vertical-lateral jerking	Stroke's F antennae	?	?	E, f	Cross and Bohart (1960); E. A. Cross, personal communication
<i>Dieunomia nevadensis</i> (Colorado)	Not mentioned ^f	Not mentioned ^f	Not mentioned ^f	Not mentioned ^f	Not mentioned ^f	No movement ^f	No movement	? ^{b,d}	22 ± 3	E, f	O'Neill and Bjostad (1987); K. O'Neill, personal communication
<i>Dieunomia heteropoda</i>	Drape over F fore-wings; no motions	Wrap around F anterior metasoma	Occasionally taps (?) F metasoma	Continuous or nearly continuous buzzing (~ 80 Hz)	Rhythmic buzzing (~ 260 Hz)	Variable; simultaneous irregular to rhythmic up-down motions, or no movement	Both moved up and down	112 ± 61	61 ± 27	E, f	Results
<i>Nomia melanderi</i>	Not mentioned	Not mentioned	Not mentioned	Not mentioned	Not mentioned	Not mentioned	Not mentioned	0	About 15	E, f	Johansen and Mayer (1976)
<i>Nomia tetrazonata</i>	On F prothorax; no motions	On F meso- or meta-thorax; no motions	No movement (frequency unknown)	None, or not audible	Rhythmic buzzing	No movement	Both moved up and down	0	14 ± 3	E, f	Results
<i>Nomia (Austrovia) sp. ?</i>	? ? ?	? ? ?	? ? ?	? ? ?	? ? ?	? ? ?	? ? ?	? ? ?	? ? ?	f	W.T.W., unpublished data

^aCross and Bohart (1960) noted that the precopulatory 'mating dance' lasts several minutes, and that copulation lasts from 8 s to approximately 1 min.
^bO'Neill and Bjostad (1987) stated that females emerge from underground with males already mounted on them; precopulatory behaviour thus would not be visible. In a Kansas population of this species, males frequently mounted females after they emerged from the soil (Kerfoot, 1964).
^cKerfoot (1964) studied a population of this species in Kansas, and stated that in all cases the mating behaviour of the bees followed a pattern similar to that described by Cross and Bohart (1960) for *D. triangulifera* in Utah.
^dIn the Kansas population, Kerfoot (1964) stated that copulation lasted \approx 1 min.
^eE, emergence site; and f, flowers.

Voucher specimens. Adult specimens of *Nomia tetrazonata*, *Dieunomia heteropoda* and *Triepeolus verbesinae* with voucher labels are deposited in the Cornell University Insect Collection (CU) (Lot No. 1216). Additional vouchers are in the University of Arizona Insect Collection, and the Snow Entomological Museum, University of Kansas.

Results

Dieunomia heteropoda

Life-history and seasonal activity. *Dieunomia heteropoda* is a large, ground-nesting bee, of which adults were active from mid-August through to the end of September in southeastern Arizona. The first males were observed on 14 August 1991, while the first females were not observed until 17 August 1991. Males began flying at approximately 07:30 h MST, or slightly earlier if the temperatures were $> 20^{\circ}\text{C}$. Males flew at a height of 5–20 cm in large numbers over areas where adult females emerged from their natal cells underground, and where females returned to their nests. After 10:00–11:00 h, males were less abundant patrolling above the nesting site. At this time males visited sunflowers (*Helianthus petiolaris* L.) to drink nectar, and attempted to mate there with foraging females. Males also spent the night on the plants' capitula (males per occupied capitulum: range = 1–7, $\bar{x} = 3 \pm 0.49$, $n = 13$). After mating, females dug nests in the sandy soil, which they provisioned with sunflower pollen and nectar (details in Wcislo, 1993). Three to 4 weeks after their emergence, males became rare at both the emergence/nesting sites and on flowers, while females continued to provision nests. By 21 September only 1 male was observed flying at the site.

Structures used in mating. Numerous structural features of *D. heteropoda* seem modified for courtship or mating, as true for many nomiine bees. The terminal flagellomeres of the antennae are flattened and broadly expanded, in contrast with the rounded cylindrical shape of the female's terminal flagellomeres. This expansion is probably not directly related to enhanced sensitivity for mate finding, since the expanded surface lacks olfactory sensilla (Wcislo, 1994).

All 3 pairs of the male's legs differ from those of the females. Blair (1935) describes some of these species-diagnostic differences, but she omits others which are given below. The following descriptions are based on a head-on view of the bee, with the legs orientated perpendicular to the longitudinal axis of the body.

The lower edge of the male's fore-femur is slightly expanded (Fig. 1a). Its anterior surface is smooth and shiny, slightly concave, with only fine, short pubescence, while the posterior surface is fringed with long, plumose hairs. These longer hairs are also present on the fore-tibia, are longest on the basitarsus, and are shorter on the next 3 tarsomeres; the antero-ventral surfaces of tarsomeres 1–4 are covered with short, stiffer hairs. The femur of the mid-leg is expanded, being conspicuously rounded on the posterior surface (Fig. 1b), with a pronounced notch near the lower end. The mid-tibia is slightly flattened, and the outer edge of the basitarsus is expanded. The hind leg has a slightly expanded femur, but a greatly expanded tibia (Fig. 1c). The hind basitarsus is elongated with a fringe of short, stiff hairs on the inner side, and the fringe is also present on the remaining tarsomeres. Expansions of the exoskeleton are associated with increased musculature, as also true for *Dieunomia triangulifera* (Wcislo, unpublished data), and as true for some other bees with enlarged hind leg segments (Toro and

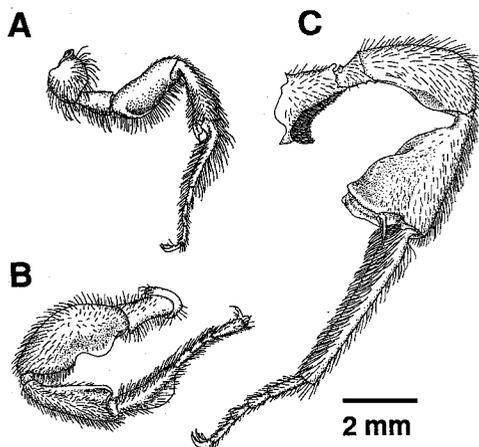


FIG. 1. Drawings of the legs of male *Dieunomia heteropoda*, illustrating secondary sexual characters. (A) Anterior view of a left fore-leg; (B) posterior view of a left mid-leg; and (C) posterior view of a right hind-leg. All figures were drawn at $12\times$ magnification. Scale bar = 2 mm.

Magunacelaya, 1987). The inner faces of the hind coxae are covered with short, fine, dense setae.

The metasoma is also modified, with sternum V having a pair of expanded knob-like protuberances (Fig. 2A,B).

Mating behaviour. Our observations were of mating pairs on the ground at the emergence site. We do not know the relative abundance of receptive females at the emergence site or on flowers. Preliminary experimental data indicate that most females only mate once (Wcislo, unpublished data), as known for other nomiine bees (see Discussion). Males frequently pounced on females at flowers, but we never observed a successful mating by bees on sunflowers ($n > 50$ males pounces on females). There were no signs of agonistic behaviour among males at flowers. The size of males flying over the emergence site (live wet weight, $\bar{x} = 0.149 \pm 0.003$ g, $n = 26$) was not significantly different from males captured on flowers ($\bar{x} = 0.142 \pm 0.004$ g, $n = 15$) (Mann-Whitney U -test, $p > 0.3$). In fact, 10 of 12 males marked with paints on flowers also were observed patrolling over the emergence site, and 8 of 15 males marked at the emergence site were later seen patrolling near flowers. Neither males collected on flowers nor those at the emergence site were significantly different in weight from males collected *in copula* ($\bar{x} = 0.145 \pm 0.003$ g, $n = 16$) (Mann-Whitney U test, $p > 0.3$).

As usual with bees, females ($\bar{x} = 0.161 \pm 0.005$ g, $n = 16$), were slightly heavier than males ($\bar{x} = 0.146 \pm 0.002$, $n = 56$ for all males pooled, $t = -3.04$, $p = 0.006$), but there was no apparent size-based assortative mating. The correlation between male and female weight for pairs collected *in copula* was not significant (Kendall's tau = 0.183, $p > 0.5$, $n = 16$).

A male pounced on a female as she emerged from her underground natal cell, or from her nest. He immediately wrapped his hind-legs around the anterior end of the female's metasoma (near sterna II or III), with the basitarsi contacting the female's sterna. The male's mid-legs sometimes wrapped around the female's metasoma (near sterna I), and sometimes the female's mid-leg was locked in the space formed between

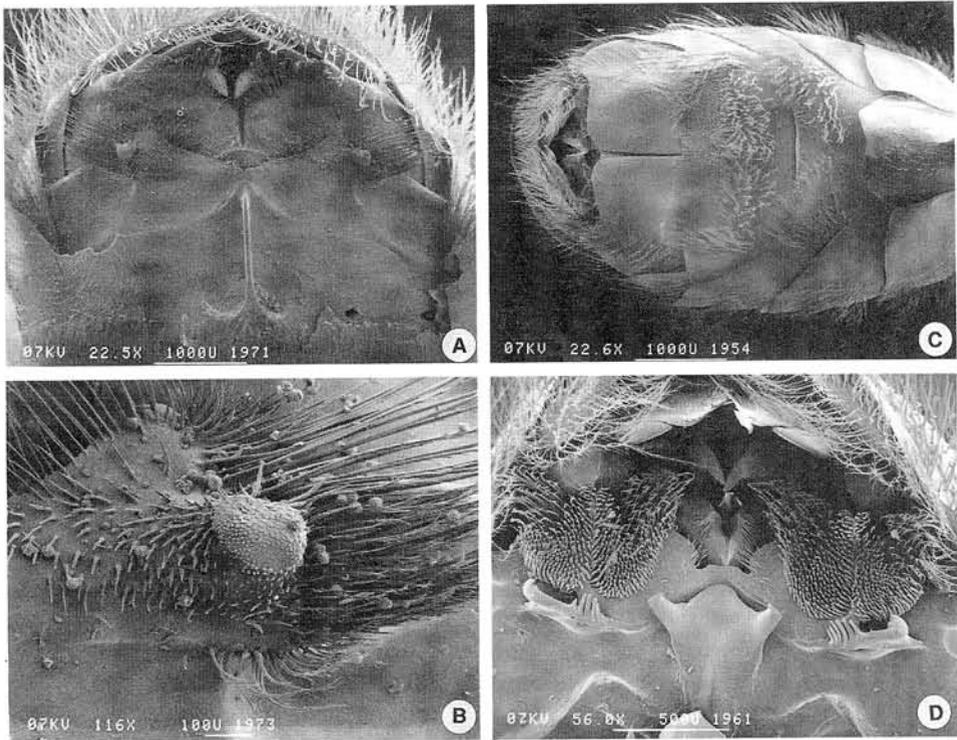


FIG. 2. Scanning electron micrographs of the male sterna of *Dieunomia heteropoda* (A and B) and *Nomia tetrazonata* (C and D). The knobs or pads shown in B and D are also species-specific in form in many other nomiine bees.

the notch in the male's femur and tibial surface. The male's fore-legs usually were draped over the female's fore-wings, with his tarsomeres hanging over the edge of the wings. None of the legs were moved in rhythmic patterns during mating.

After being mounted by a male, the female usually walked over the ground in an apparently random pattern, sometimes making biting motions at the male's mid- or hind-legs. Other males frequently flew at, and collided with, the mating pair, but we never observed one male dislodge another one.

While situated on a female, the male held his antennae straight out, but did not contact the female with them. The occurrence of antennal movements and vibrations during pre-copulatory courtship varied among individuals, and even by an individual during a single mating attempt (Fig. 3). Based on analyses of videotapes, in some cases (12 of 25) the male usually kept his antennae still, at least during the initial stages of courtship. Approximately half of the males (11 of 25) occasionally moved both antennae in an up-and-down motion, but not in a simple rhythmic pattern. The down-stroke lasted an average of 0.16 s (SE = 0.012, $n = 30$), and the up-stroke plus the pause between strokes lasted 1.5 s (SE = 0.52, $n = 30$). Two males consistently and regularly moved their antennae, at a rate of about 1 per s.

Occasionally during pre-copulatory behaviour, the male made slight 'tapping' motions with his metasoma which contacted the female's metasomal terga. It was not clear if these motions were in fact 'tapping' movements (as in *Dieunomia triangulifera*; Wcislo *et al.*, 1992), or whether they were simply motions by which the male attempted

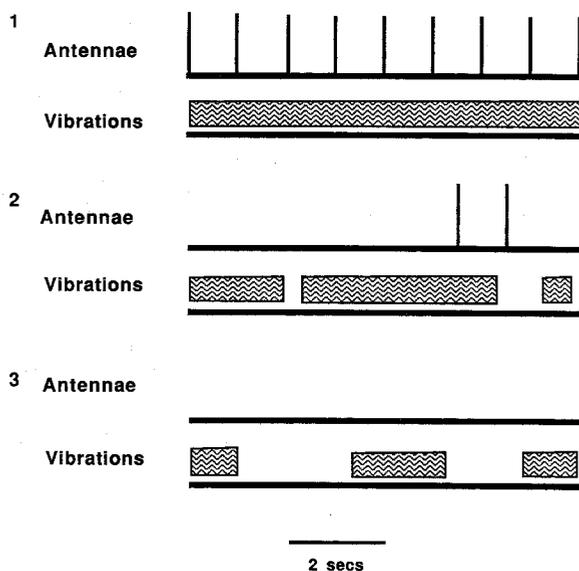


FIG. 3. Schematic descriptions of the precopulatory behaviour of three males of *Dieunomia heteropoda*. Some males (e.g. #1) moved their antennae regularly and consistently, while others (e.g. #2) moved them intermittently, and still others (e.g. #3) kept them motionless before mating. Some males produced vibrations continuously (e.g. #1), while others only made sporadic vibrations (e.g. #2 or #3).

to make genital contact with the female. The latter interpretation may be more plausible, since in 4 cases it was possible to see that a male had partially everted his genitalia prior to intromission.

During the precopulatory phase the male sometimes flicked his wings, which shimmered in the bright sunlight. These wing motions were associated with very low-frequency vibrations, which were audible to us as faint buzzing or 'rumbling' sounds. In some males these vibrations were produced almost continuously, while in others they were produced intermittently, and still other males did not produce such vibrations prior to copulation (Fig. 3). These pre-copulatory vibrations are made at a frequency of approximately 80 Hz (at 30°C) (Fig. 4b), which is slightly lower than the mean wing-beat frequency (95 Hz) at the same temperature (Fig. 4a). The precopulatory phase lasted from 9 to 240 s ($\bar{x} = 112.7 \pm 18.43$, $n = 11$; based only on pairings seen from beginning to end). Frequently, towards the end of the precopulatory phase, just prior to intromission, or prior to their separation if the female is not receptive, the pair flipped upside-down (11 of 17 successful mating attempts; 4 of 8 unsuccessful ones). We presumed that it was the behaviour of the male which flipped the pair, since the female rapidly moved her legs through the air with walking movements, and appeared to struggle to right herself, and often bit the male's legs.

If a female was receptive, a male inserted his genitalia, which were rapidly thrust into the female (duration, $\bar{x} = 0.1 \pm 0.0001$ s, $n = 39$), and then withdrawn more slowly, followed by a brief pause before another thrust ($\bar{x} = 0.71 \pm 0.023$ s, $n = 39$). Each thrust-withdraw-pause sequence lasted on average about 1 s ($\bar{x} = 0.8 \pm 0.024$, $n = 39$), and there was significant variation among males (ANOVA, $F_{(3,35)} = 4.298$, $p = 0.011$, based on males measured within $\pm 1^\circ\text{C}$). The male also simultaneously moved both antennae up and down at a rate of slightly > 1 per s ($\bar{x} = 0.7 \pm 0.016$, $n = 10$ movements from each of nine males). There is significant variability among males in this rate

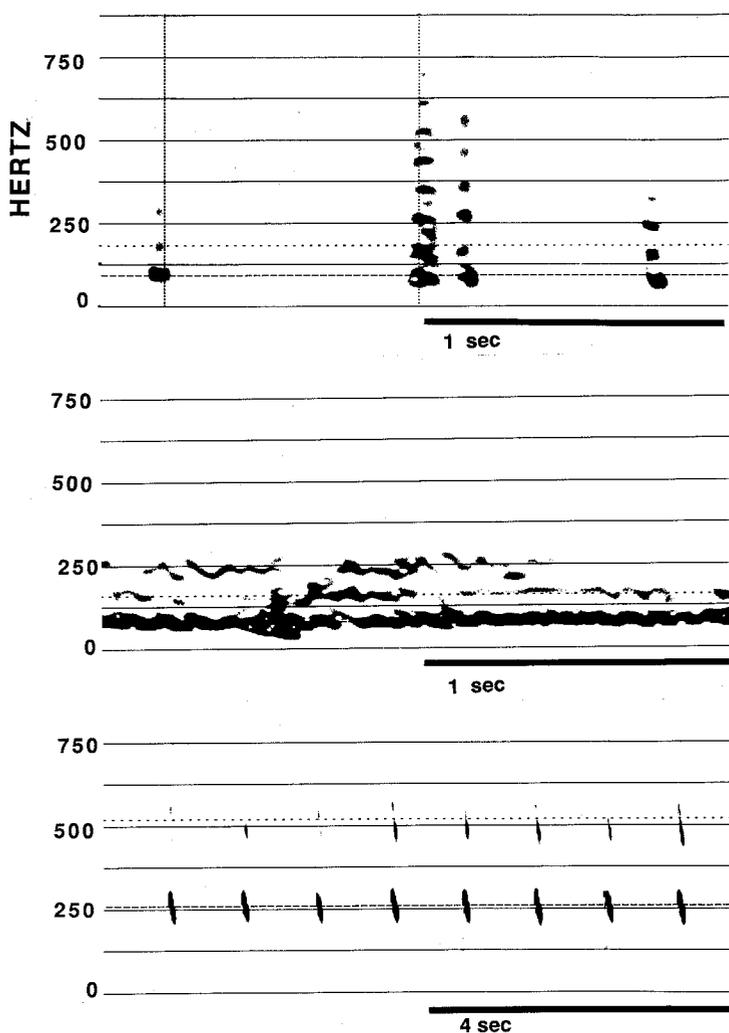


FIG. 4. Representative sonograms of wingbeat frequencies (top) of male *Dieunomia heteropoda*; vibrations made while a male is mounted on a female but prior to copulation (middle); and vibrations made while a male is copulating (bottom).

(ANOVA, $F_{(8,81)} = 6.313$, $p < 0.001$). During these antennal movements the head also made a very slight up-and-down movement. Infrequently, the male relaxed his grip on the female's metasoma, and the hind-legs moved slightly forwards and back, coincident with the up-and-down motions of the antennae respectively. The in-and-out movement of a male's abdomen was accompanied by a rhythmic buzz of higher-frequency vibrations (260 Hz), which occurred at about 1 per s (Fig. 4c). There were no other obvious motions made by the male or female. Copulation lasted from 24 to 129 s ($\bar{x} = 60.7 \pm 14.72$, $n = 17$), after which the male released the female and flew away.

Nomia tetrazonata

The bees nested in an arc around what was the northwest shore of Mormon Lake (the lake was dry at the time of this study), and males were abundant over an area roughly $10 \times 140 \text{ m}^2$ (Wcislo, 1993).

Structures used in mating. Males of *Nomia tetrazonata* have many of the same the structural modifications seen in *D. heteropoda* (see Ribble, 1965), except that the terminal flagellomeres of the antennae are not broadly flattened, and have numerous sensory sensilla (especially sensilla placodea) over the entire surface (Wcislo, 1994). The hind-legs are modified in ways similar to *D. heteropoda*, except that they are not expanded to the same degree (Ribble, 1965), and the hind coxae are not covered with a dense carpet of pubescence. The mid-trochanter is covered with fine, dense pubescence, and the femora are expanded, but not notched as in *D. heteropoda*. The femora of the fore-legs are slightly expanded, and the lower edge of the tibia is flattened distally, but has no elongate hairs. Sternum V of the metasoma also has a pair of knob-like protuberances, but they differ in shape and texture from those of *D. heteropoda* (Fig. 2C,D).

Mating behaviour. Males slept on vegetation (mostly *Polygonum pennsylvanicum*) within the area where females nested, and they began flying at approximately 07:00 to 08:00 h MST, or earlier when the temperature rose above approximately 24°C. Males patrolled over the site where females were nesting and emerging, at a height of < 20 cm, and also patrolled among nearby vegetation. They also occurred on more distant mesquite trees when those were in bloom, where they both patrolled and drank nectar. Males often ($n > 30$ observations) pounced on females without pollen, but rarely pounced on females entering nests with pollen ($n = 6$ pounces during > 200 observations of females entering their nests with pollen). We observed successful copulations only six times and, in each case, a male pounced on a female as she emerged from her natal nest. The male immediately wrapped his hind-legs around the female's anterior metasoma, and placed his front legs on the female's prothorax; the mid-legs stood on the female's meso- or meta-thorax. The male's antennae were directed anteriorly, and did not contact the female's antennae. None of these appendages were moved prior to intromission, nor were there any vibrations audible at the distance we observed them (approximately 1 m). Very quickly after contacting a female (< 5 s), a male inserted his genitalia if the female was receptive; in numerous cases a male quickly (< 5 s) left an unreceptive female. Mating was relatively brief (duration, $\bar{x} = 13.7 \pm 1.333$ s, $n = 6$), as with some other halictids. During copulation the male's antennae were moved synchronously up and down, about 1 s^{-1} . The male made clearly audible rhythmic buzzes, approximately 1 s^{-1} (frequency unknown), apparently coincident with thrusting his terminalia into the female. After mating, the pair split up, and the male flew off.

Tripeolus verbesinae

The following anecdotal observations are worth reporting since the mating behaviour of parasitic bees is so poorly known. Females of this species are cleptoparasites which attacked nests of *Nomia tetrazonata* at the BANWR site (Wcislo, 1993).

Structures used in mating. Males of this parasitic species have no obvious secondary sex characters, except that metasomal sterna IV and V have an apical fringe of long, curly setae.

Mating behaviour. Males were extremely abundant flying over the nesting site of *N. tetrazonata*. On 24 July > 150 *T. verbesinae* males were each marked with a dot of paint, and hundreds more remained unmarked. The large numbers of males flew over the nesting site at an altitude of 6–10 cm, searching for the apparently less abundant females, which were flying even nearer to the ground surface, searching for nests. Most males that pounced on females were rejected, but one copulation was observed. The pair was first observed *in copula*, with the male atop the female; his hind-legs held motionless and parallel to the female's metasoma; his fore-legs held on her prothorax (the position of his mid-legs could not be discerned); his antennae were directed anterior and not contacting the female; and his metasoma was rhythmically contracting. After five more contractions the male withdrew his genitalia, and then with his genitalia still everted, he made tapping motions (42 taps at a rate of about 1 per s) on the female's metasomal terga (whether the male contacted the female with genitalia or metasoma was not clear). While tapping, both of the male's antennae moved rhythmically up and down, again about 1 per s.

Discussion

Erroneous assumptions which underlie the perceived antithesis between 'form' and 'function' are difficult to correct, because biologists who are primarily concerned with the former are often not concerned with the latter, and vice-versa (Russell, 1916; Woodger, 1929). Courtship behaviour is especially informative for integrating form and function studies. In a sexual context the 'environment' in which characters function for current utility is obviously created by conspecifics (Wcislo, 1989). Likewise, the secondary sexual characters themselves obviously preserve historical information since they are so frequently used by taxonomists and systematists to understand evolutionary patterns (for discussion see Eberhard, 1985, 1991).

The courtship behaviour of some nomiine bees stands in contrast to that of most bees previously studied, which usually have no precopulatory courtship, and little copulatory courtship (references in Wcislo *et al.*, 1992; see discussion in Eberhard, 1991). A striking feature of male nomiines is their array of elaborate secondary sexual structures. With exceptions (e.g. *Agapostemon*), such structural modifications are absent among males in the sister taxon to Nomiinae, the Halictinae. Males of some species in the Rophitinae, which presumably gave rise to the clade of Nomiinae + Halictinae, have various secondary sex modifications, but their mating behaviour is also little known.

Some information on male behaviour is known for six species of Nomiinae (Table 1), all of which have similar structural modifications, with the exception that only male *D. heteropoda* has strikingly modified antennae. One of the two more pronounced modifications are the enlarged hind tibiae of males, which in all cases are wrapped around the female's metasoma. The placement of these structures on the female's body apparently prevents a male from being knocked off, and prevents the female from otherwise escaping the male's grasp (Results; O'Neill and Bjostad, 1987; Wcislo *et al.*, 1992). Since insects can detect deformations and stresses in their exoskeleton (Chapman, 1982), male structures which apparently clasp a female may in fact be stimulating, as shown for male structures in damselflies (Odonata) and fairy shrimp (Anostraca), which were previously believed to have a clasping function (Robertson and Paterson, 1982; Belk, 1984). Similarly, all species also have metasomal

modifications (Fig. 2), which may have sensory or glandular functions (see Youssef, 1969).

Various ethological traits vary among the species studied. The use of antennae varies markedly. Males of *D. triangulifera* rhythmically move their antennae as a part of pre-copulatory behaviour, and keep them motionless during copulation; males of *D. heteropoda* sometimes move their antennae before copulation, but always make antennal movements during copulation; while males of a population of *D. nevadensis* make no antennal movements either before or during copulation. In the Halictinae, such behaviour also apparently evolves sporadically. Plateaux-Quénu (1992) observed that males of *Lasioglossum (Evyllaesus) alpibes* hit the head and thorax of females with their antennae during copulation, while *L. (E.) calceatum* do not do so; these two species are hypothesized to be sister taxa (Packer, 1991), and at least 1 of the outgroup taxa [*L. (E.) malachurum*] lacks any obvious courtship behaviour (Laurence Packer, *in litt.*).

None of the pre-copulatory tapping or stroking behaviour seen in *D. triangulifera* was observed in any of the other species, including *D. heteropoda*, which has very elongate or brush-like hairs on the fore-legs and hind-legs respectively. Without further comparative and experimental data functional interpretations are speculative.

The mate-searching strategies differ among species and among populations. Males of all the New World species for which information is available fly over the previous season's nesting area from which females emerge, while males of *N. (Austronomia)* sp. leave the emergence site and patrol on flowers. In this study, males of *D. heteropoda* were never observed successfully mating with females at flowers, while Hurd *et al.* (1980) state that 'mating takes place on the flowers and other males frequently attempt to dislodge the first male to achieve copulation' (p. 60). Males of the parasitic bee, *Triepeolus verbesinae*, also flew over the nesting site, as do males of *T. distinctus* (Wcislo, unpublished data), while Alcock (1978) noted that males of *Triepeolus* sp. (P.D. Hurd, *in manuscript*†) patrol regular routes among vegetation. All *Triepeolus* studied have some copulatory courtship behaviour (Results; Alcock, 1978).

Interspecific differences in behaviour and structure among nomiine bees appear to lend support to notions that such characters evolve under social competition for access to mates, or for inducing sexual partnership (West-Eberhard, 1991; Eberhard, 1991). Based on present (limited) ethological knowledge, female nomiines mate once, or infrequently a female mates a few times (O'Neill and Bjostad, 1987; Wcislo *et al.*, 1992), indicating that opportunities for female choice may be evolutionarily rare (for genitalic correlates, see Roig-Alsina, 1993). Comparative studies of mating in nomiine bees suggest that elaborate secondary sex characters, once evolved, may have current utility in ways difficult to predict.

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†According to Alcock (1978), P.D. Hurd believed the bees were an undescribed species; the manuscript describing this species was never published before Hurd's death.

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