

Notes on Male Mate-Locating Behavior in Some Bees and Wasps of Arizona

(Hymenoptera: Anthophoridae, Pompilidae, Sphecidae, Vespidae)

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Relatively little is known about the reproductive behavior of male bees and wasps. Yet even from the limited data available it is clear that the diversity of mate-locating strategies exhibited by males of these groups is impressive (Alcock et al., in press). Through comparative studies it may be possible to determine why so many different kinds of mating adaptations have evolved in the Hymenoptera. This paper provides brief descriptions of male behavior in five species of bees and wasps for use in future analyses of the relation between the reproductive behavior and ecology of these insects.

The research was done at three study sites in southeastern Arizona. Study site 1: A flat plain about 1 km north on the road to San Simon near Portal, Arizona (Cochise County) at an elevation of about 1600 m. The area was covered with a relatively dense stand of creosote bush. For a full description of the flora in this region see Linsley and Cazier (1972). Study site 2: A dry stock tank 1 km to the north of Study site 1. The floor of the tank was partly covered with a flowering shrub, *Baccharis* sp., which was attracting many Hymenoptera. The earthen bank of the stock tank had a sparse cover of shrubs and gourds. Study site 3: A ridge in the Chiricahua Mountains 2 km to the south of Portal, Arizona at an elevation of about 2100 m. Peaks along this ridge supported scattered shrubs and small pines.

Some individuals of all the species studied were captured and given distinctive color marks of acrylic or enamel paints on the dorsum of the thorax. Records were then made of the activities of known individuals. A stop watch was used to time the duration of flights from perches or along patrol routes.

Voucher specimens of the undescribed species have been placed in the entomology collection at Arizona State University.

Results

Triepeolus n. sp. (in manuscript) (det. by Paul D. Hurd, Jr.)

Males of this parasitic anthophorid bee were observed at study site 1 from 3-15 August 1977. Individuals patrolled regular routes through creosote bush stands from 0730-1330. They flew rapidly, briefly visiting bushes that were an average of 8.1 m apart (N = 19; range = 4.8 - 24

m). Upon reaching a creosote station on its route a male would usually slow somewhat and spend 1-3 sec circling over a portion of the bush, almost always $\frac{1}{2}$ -1 m above the ground, before flying on to the next inspection point. On three occasions, all between 0815-0845, a male alighted on creosote leaves on what proved to be a regularly visited station and walked quickly over the foliage in a small area (probably applying a pheromone in the process). If this was pheromone-marking behavior, one brief (less than 5 sec) application lasted for at least one morning.

The routes of males must have been roughly circular because recognizable individuals always appeared at a station moving in the same direction. The interval between visits to the same station averaged 8.3 min ($n = 20$, Male "White"), 8.3 min ($n = 7$, Male "Pink"), 9.3 min ($n = 7$, unmarked male), 12.0 min ($n = 9$, Male "Red-White"), and 9.8 min ($n = 16$, unmarked male). I estimated conservatively that a male required 5 sec to travel 10 m and to inspect one station. Assuming this rate of travel and taking the minimum time between two visits to a bush as the time needed to fly around the entire route, these five males covered patrol routes with a circumference of at least 450-600 m. Because of the difficulty of following the rapid, low-flying males through the creosote stand, I was never able to trace the path of a male for more than 80 m.

Some males followed all or a portion of the same route over a period of days with White, Pink and Red-White seen at one of their stations on two consecutive days. Pink visited the same inspection point on 4-6 and 8 August.

There was substantial overlap in routes travelled by different males. On numerous occasions two males were seen at the same station, sometimes almost simultaneously. Three marked males were seen at one bush on 5 August. Often males arrived at an inspection site from different directions but some individuals followed the same routes for at least four inspection points.

The behavior of this species of *Triepeolus* resembles the behavior of those male bumblebees that mark vegetation at intervals along a "trapline" which they patrol (Free and Butler, 1959; Kullenberg et al., 1973). Bumblebee females wait at an inspection point and copulate with a male that finds them. This is probably true for this *Triepeolus* as well. I collected conspecific females foraging at creosote bushes and crushed their thoraxes. The immobilized individuals were placed on the foliage at stations visited by males. Some specimens elicited no response but on six occasions, a male located the female (usually after circling slowly in and around the portion of the creosote bush on which she had been placed) and attempted copulation. When a male landed on a female's back, he quickly oriented himself so that his head was above the female's head. He then stroked the female with his legs and antennae, while his abdomen rhythmically tapped the

female's abdomen and his wings whirred in synchrony with the rapid stroking and tapping movements. This pattern is similar to that of the anthophorid *Centris pallida* Fox (Alcock et al., 1977) and the oxaeid *Protoxaea gloriosa* (Fox) (Alcock, pers. observations).

The slow circling flight of males as they zeroed in on a female indicated that they may initially use an odor cue to detect a female that has landed at a station. Additional evidence for this possibility comes from four observations of males circling and hovering for over 5 sec in the vicinity of creosote leaves from which a female specimen had recently been removed. In one case, a male actually alighted on leaves from which a female specimen had been removed some minutes previously.

Nomada n. sp. (det. by R. R. Snelling)

This is an undescribed species near *N. gutierreziae* which was observed at study site 2 between 3-7 August 1975. Males of this anthophorid bee also appear to have a patrol route many meters in length with stations that they visit and mark. Tengo and Bergstrom (1977) report that males of some European species of *Nomada* follow patrol routes used by males of the host species parasitized by their females. I located a single station at the top of an earthen bank of a stock tank in an area with cucurbit gourd ground cover and a few stalks of grass about 15-25 cm high. A male that visited the site would circle slowly in the vicinity of two grass stalks about 1 m apart before flying to and alighting upon one or the other of these plants. It then walked quickly up the stem and along the curving blade of the grass with its abdomen and head held close to the substrate (Fig. 1). After walking a distance of about 10 cm it would fly off so quickly that I was unable to follow the male to any other station. Tengo and Bergstrom (1977) do not mention marking of vegetation by European *Nomada* although they did find that males applied chemical substances to the backs of females during copulation. These odors mimic those of the species of *Andrena* parasitized by the female *Nomada* and may permit the female to gain access to a host nest more easily. The behavior of

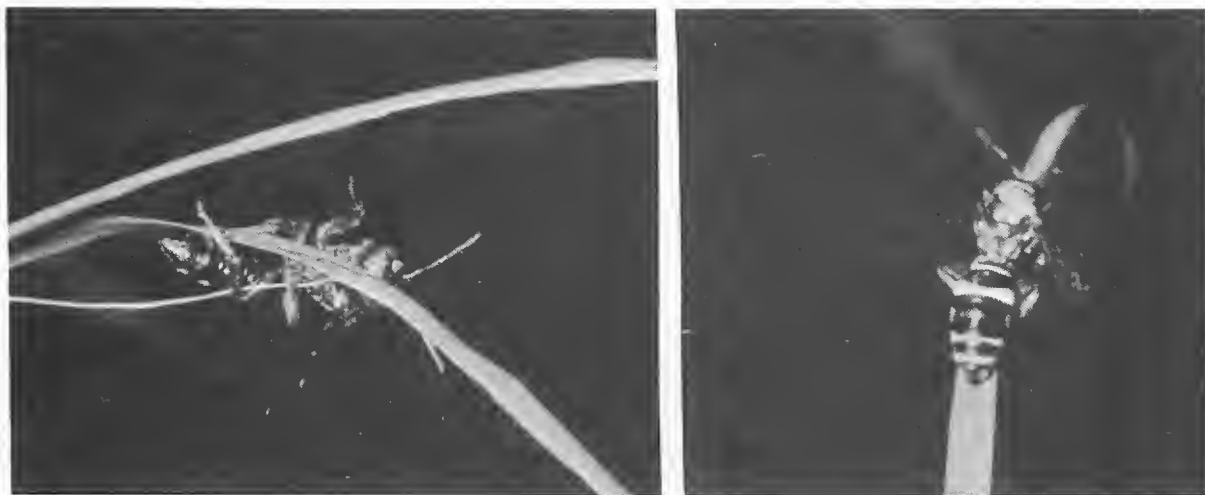


Fig. 1. Two views of a male of an undescribed species of *Nomada* walking along grass blades that were visited repeatedly by this and other males.

males of European *Nomada* may be derived from marking substrate with an odor similar to an *Andrena* host in order to lure a female to a site where she might be found and induced to copulate.

The two grasses were visited primarily by one male "Orange" that returned to the station at an average interval of 181 sec on 5 August (N = 10; 0840-0925; range, 90-445 sec) and 242 sec on 6 August (N = 11; 1015-1100; range, 70-355 sec). On its first visit of the day on 5 August it marked both grass stems four or five times and remained in the area for several minutes. Thereafter it marked one grass stem once or twice and left after less than 30 sec. Although Orange was the primary visitor, other males were seen at the site on three of the five mornings of the study. When Orange was collected a new male became a regular visitor on the following day. Thus as in *Triepeolus* and the trap-line visiting bumblebees, more than a single individual may come to the same station(s).

Philanthus gibbosus (Fabricius) (det. by H. E. Evans)

Males of this sphecid wasp were observed at study site 2 from 2-8 August 1975. The behavior of male *Philanthus* has been reported in some detail for a number of species (Simon Thomas and Poorter, 1972; Alcock, 1975 a, b; Evans 1975). Although Evans (1973) found that males of *P. gibbosus* spend the night in nests occupied by their sisters, he did not discuss male reproductive behavior. I found 2-4 males of this species on each day between 2-8 August at a cluster of yucca stalks on the earthen bank of the stock tank. Individuals perched at heights of 2-2½ m on dried branches or twigs (Fig. 2) and were separated by about 1½-3 m. The wasps regularly flew out from their perches (usually 2-3 times per min) for an average flight of 5.6

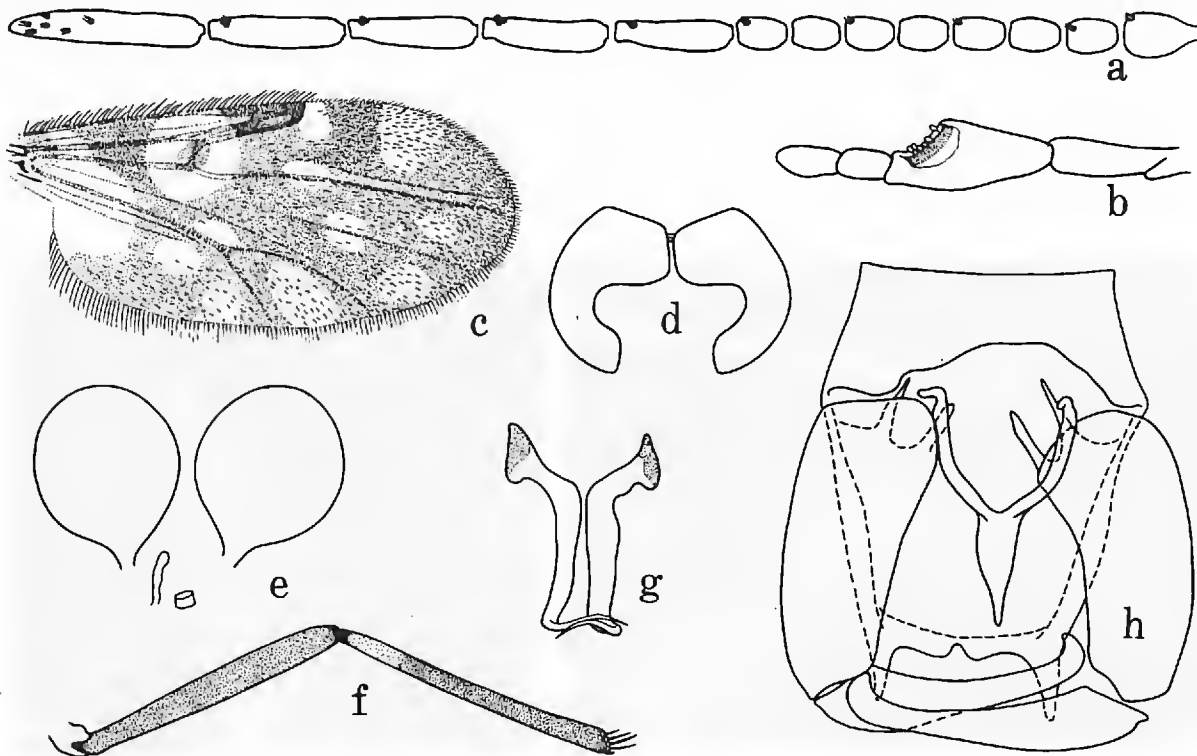


Fig. 2. A male of *Philanthus gibbosus* at its territorial perch on a yucca stem.

sec ($N = 54$; range 1-25 sec) before returning. Upon landing the male was likely to pump his abdomen up and down while standing on the perch or walk along the stem dragging the venter of his abdomen on the substrate for several cm (see Fig. 7, Alcock, 1975a). This behavior may be associated with the deposition of a sex pheromone (Alcock, 1975a) although during approximately 14 hr of observation no copulating pairs nor any females appeared in the vicinity of the perches. Perch owners did attract other male "visitors" (Simon Thomas and Poorter, 1972; Alcock 1975 b). The resident male flew off his perch at the approach of a visitor or visitors (up to three intruders were seen simultaneously at a perch site) and pursued the interloper(s). Males of *P. gibbosus* interacted with little or no physical contact, restricting themselves to simple chase flights. Visitors often remained for several minutes before finally being driven off or departing of their own volition. On two occasions a marked resident male was replaced at its perch by another individual after an interaction between them.

Males claimed perch sites in the early morning (0800-0930) and might remain until midday. Records of marked males show that individuals held their territories for an average of about 2.2 hrs per day (with a maximum of 3.5 hrs; $N = 7$). There was a high daily turnover of males at the site. Of eight marked individuals only two appeared at perch for more than one day (one male for two days and another for four days). Apparently there were many males floating through the area judging from the number of visitors. On 7 August at midmorning I removed a resident male from each of four yucca stalks and on the next day two of the stalks were held by new males.

The social system of male *P. gibbosus* is similar to that of several other philanthine wasps (Simon Thomas and Poorter, 1972; Alcock, 1975a; D. L. Gwynne, pers. communication). Males of these species form small aggregations of pheromone-applying, territorial individuals that rarely spend more than a few hours at their perches. Territorial sites are attractive to other males with several visitors inspecting the perch on any given day and the same perch occupied by different males on each of several days in succession. Perch sites are located near flowering plants or near small diffuse clusters of nesting females. One active nest of *P. gibbosus* was found within a few m of the yucca perch area.

Hemipepsis ustulata ochroptera Stål (det. by P. D. Hurd, Jr.)

Males of this pompilid wasp were studied between 14-19 August 1977 at study site 3. They were found exclusively on three peaks along a mountain ridge behind Portal, Az. and behaved like a typical "hilltopping" insect (Shields, 1967). The tarantula hawk males perched on the tips of pine needles on the stunted, flat-topped pine trees on the peaks. As many as seven males were seen, each on a separate tree, during one morning at one peak. Males were active between at least 0830-1200 and on one afternoon excursion to the site I found a few males present at 1800.

Males flew out from their perches at irregular intervals looping around the tree several times, usually to inspect or pursue a passing *Hemipepsis* from another tree. Normally interactions involved only a brief period of pursuit in horizontal flight followed by the separation of males and their return to their respective perches. Despite the customary absence of overt aggression, this species is clearly territorial as shown from the following observations:

- (1) Never more than a single male occupied the same tree top (areas of 3-5 m²).
- (2) Three of five males that were marked on 14 August held the same tree tops on subsequent visits to the area on 16 and 19 August. (The other two males were not seen again.)
- (3) When a male (White) on the highest tree on the peak was captured and held in a net, its tree top was occupied within 7 min. by an unmarked male. After 5 min. more, White was released and immediately returned to its perch area. There followed a series of elaborate aerial duels between the two males. These began with the horizontal circling chases that occur among established resident males. The chases quickly led to steep spiral flights with the two males side-by-side (so close that wing clashing often occurred). After reaching a height of 10-25 m, the two *Hemipepsis* broke off the encounter with first one and then the other diving back to the perch tree. Within 4 min., White had replaced the unmarked male although 10-15 additional vertical flights were seen after White had regained control of the tree.

Transient males were regularly seen. They usually perched in a tree top for a short time and interacted with nearby resident males. They then left. Desirable territories were evidently in short supply despite the availability of unoccupied trees; I removed resident males from four trees on 19 August and within 4-11 min. three of the trees were taken by a replacement male. There was some evidence that the higher the tree, the more desirable it was as a territory:

- (1) Males never perched in trees on the lower half of the peaks or on trees on the saddles between peaks.
- (2) The two marked males that did not return to their perches were captured on the two lowest trees of the five pines that were occupied on 14 August.
- (3) I assume that one of the factors that determines the ability of males to gain and hold a desirable territory is the size of the individual. This is true for many territorial invertebrates (e.g. Potter et al., 1976; Hamilton et al., 1976; Alcock et al., 1977). If this holds for *H. ustulata* very small males may be forced to occupy inferior sites. There was substantial size variation among territorial males. The three smallest individuals of 11 collected males had head-widths of 3.85-4.20 mm vs. 4.50-5.05 mm for the

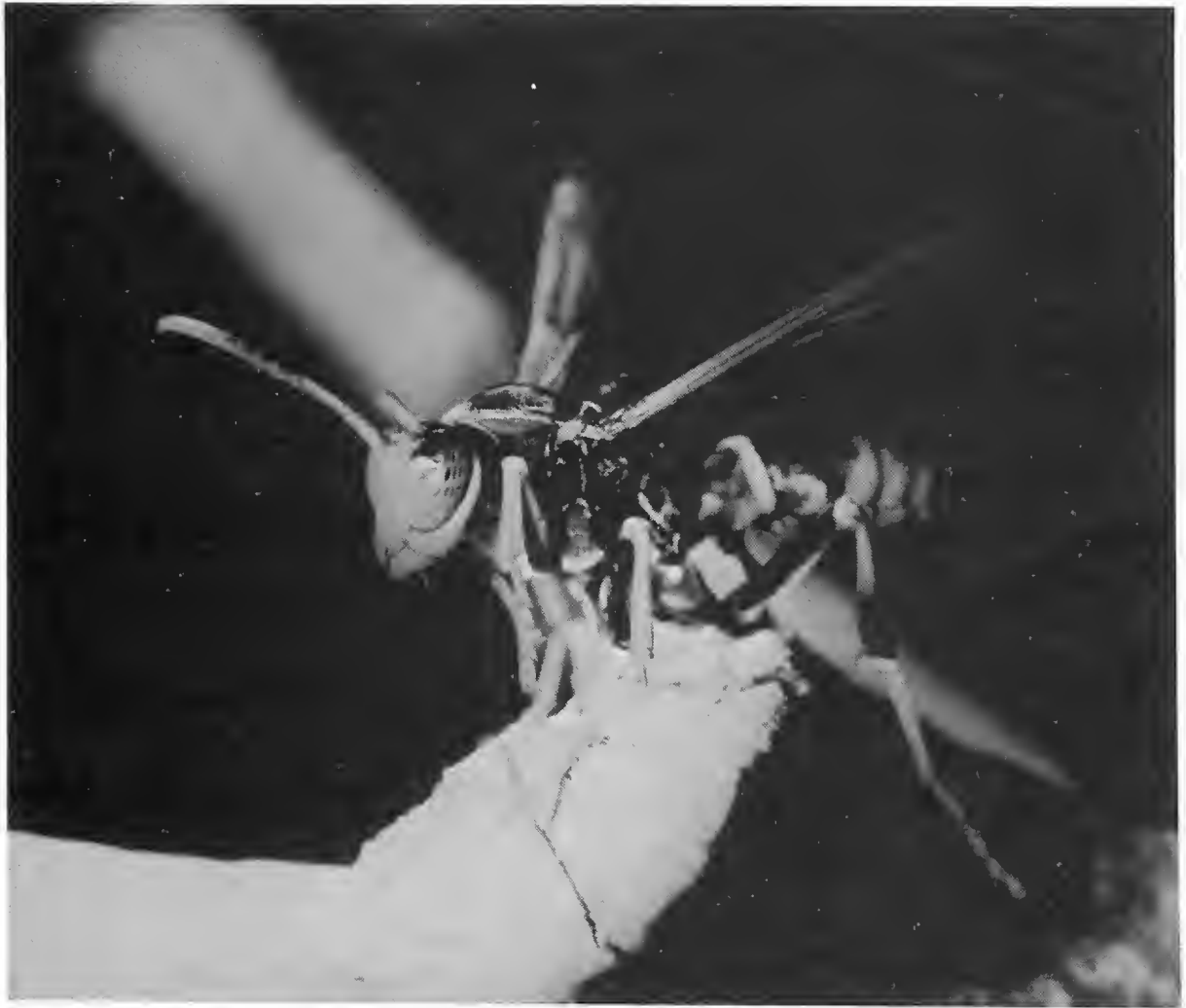


Fig. 3. A male of *Polistes canadensis navajoe* at its territorial perch at the tip of a dead pine branch.

others; all three were captured on trees well down the slope of the peak below the other eight males.

No copulations were seen nor were any females observed at the peaks, although a few were seen searching for prey on mountain slopes in the Chiricahuas.

Polistes canadensis navajoe Cresson (det. by R. M. Bohart)

This vespid was observed on the same peaks occupied by *Hemipepsis* males between 14-19 August 1977. Eberhard (1969) and Lin (1972) have described territorial behavior in several species of *Polistes*, including a different subspecies of *P. canadensis*, in which males defended perches near nest sites and hibernation areas. The males I watched held territorial perches on dead pine branches (Fig. 3), yucca stalks, rocks and patches of foliage on living pines and other shrubs. The diversity of the perches and the exposed nature of the peaks makes it unlikely that these wasps were defending hibernation areas or any other resource of value to females.

During the major period of activity (1000-1900) dozens of males were present in the area. They constantly made short forays out from their perches which were separated by a meter or two. Usually these flights occurred when another *Polistes* flew within several meters of

their perch, although *Hemipepsis* males were repeatedly pursued and struck in flight and even butterflies were approached. Intraspecific encounters generally involved fairly slow sinuous flight chases without contact. Because several males often occupied the same tree, when one male flew up others were likely to join one by one in the chase forming an aerial conga line with all participants returning to their home perches within 15-30 sec. Sometimes however wing clashes occurred. More rarely males butted heads in flight and fell to the ground to grapple together. Four prolonged struggles with much biting and wrestling were seen.

Marked territory owners exhibited strong site tenacity. Of 12 males captured and marked on 14 August, 10 returned to their perches promptly that day, 9 were seen again on 16 August and 8 were at their territories on 19 August.

One copulation was observed at 1005. A female was seen after she had arrived on a branch in a male's territory. The male quickly scrambled onto her back. He probed with the tip of his abdomen and soon achieved copulation which lasted less than 30 sec. The pair then separated (perhaps disturbed by my approach) and the female flew off.

Discussion

The reproductive behavior of these five bees and wasps is the product of selection for (1) the ability of males to compete with one another for access to females and (2) the ability of males to locate productive areas in which to search or wait for mates. The competitive component of male behavior is most obvious in the territorial species in which individuals seek to exclude others from perch sites. At least some males in the populations of *P. gibbosus*, *H. ustulata* and *P. canadensis* in the Portal area appear to be forming leks in which aggregated males compete for ownership of purely "symbolic" territories. Defended sites in lek species do not in themselves contain females or a resource that draws females to the area. However receptive females may visit the lek to select a male that has demonstrated his dominance abilities in competitive interactions with other males. Leks may evolve when males are unable to monopolize females directly (e.g. by guarding an emergence area) or indirectly by controlling resources (such as a nest site or nectar sources) that females require (Emlen and Oring, 1977).

The competition among males of the *Nomada* and *Triepeolus* bees was more subtle. They patrolled such a large area that they could not possibly exclude conspecific males from their searching route and they did not attempt to do so. But perhaps the male visitors that came to an inspection point were exploiting the male that marked the station by seeking to intercept a female attracted to the area by his pheromone.

Males of all bees and wasps presumably compete for the best locations in which to find potential mates. For many species this means searching at emergence sites and mating with emerging virgin females (Alcock et al., in press). But for all five species whose behavior has been described here, emerging females may not be easy to locate because they are probably not clumped spatially. Females of *Hemipepsis* nest where they can find an appropriate spider burrow and victim (Williams, 1956). *Polistes canadensis* are not uncommon but their nests are scattered and the emergence of future queens occurs over a period of weeks (Eberhard, 1969). *Philanthus gibbosus* does sometimes form dense nesting groups (Evans, 1973) but in the Portal area the species is uncommon and nests appear to be distributed in ones and twos over a broad area (Cazier and Mortenson, 1965). The species of *Nomada* and *Triepeolus* are almost certainly sparsely distributed; females may emerge from whatever host burrow their mother happened to locate. Therefore in these species, males resort to alternate patterns of mate location. The wasp species gathered at conspicuous landmark beacons (yucca stalks on an elevated bank, rocks and vegetation at the top of isolated hill tops) in the vicinity of nesting habitat of their species. The *Philanthus* lek was near a nest of a conspecific female. Female *Hemipepsis* were seen on mountain slopes searching for prey and female *Polistes* nest in rock crevices on mountainsides.

The two parasitic bees employed the very different alternate strategy of cruising around a circular route looking for females attracted to their pheromone stations. Male *Triepeolus* patrolled trap-lines in areas with flowering creosote bushes visited by conspecific females and their hosts. Males of the European species of *Nomada* patrol areas in which females of the host species are nesting (Tengo and Bergstrom, 1977).

The landmark and trap-line strategies are employed by other male bees and wasps whose females are scarce and widely dispersed (Alcock et al., in press). Perhaps the landmark strategy evolves in those species whose scattered females have a tendency to search elevated areas (be they banks, hills or mountain peaks) for flower resources, or prey or nesting habitat. Males that gather in such areas and advertise their presence and competitive ability through pheromones or conspicuous flight patterns may have better-than-average chance to encounter a receptive female.

The trap-line method may evolve in species whose females have no preference for conspicuous topographical features in their environments. Here the superior strategy may be to spread a net of pheromone marked stations through habitat likely to be visited by females searching for food or for potential hosts.

Summary

Male mating strategies are described for five species of bees and wasps found in southeastern Arizona. This is the first report of male reproductive behavior for representatives of the genera *Triepeolus* and *Hemipepsis*. Males of the wasps *Philanthus gibbosus*, *Hemipepsis ustulata* and *Polistes canadensis* gather at landmark sites and form lek-like assemblages in which males compete for control of perch territories. Males of undescribed species of *Nomada* and *Triepeolus* patrol routes through habitat which may contain flowers visited by potential mates or nests of the host species parasitized by their mates. Both strategies may arise because receptive females are scarce, dispersed, and difficult to monopolize directly or indirectly through control of a localized resource valuable to females.

Acknowledgements

I thank H. E. Evans, R. M. Bohart, R. R. Snelling, and P. D. Hurd, Jr. for their willingness to identify specimens for me. Douglas Whitman graciously assisted me in my observations of *Triepeolus*. This work was supported by National Science Foundation Grant DEB76-04503-A01.

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