

Hilltopping Behavior by Three Species of *Tachytes* Wasps (Hymenoptera: Crabronidae)

JOHN ALCOCK

School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501

ABSTRACT: Although hilltopping behavior has rarely been reported for crabronid wasps, three species of *Tachytes* wasps defend hilltop perch sites in central Arizona during the late summer. All three species (*T. ermineus*, *T. spatulatus*, and *T. sculleni*) can be found at the same hilltop during August and September and they perch in many of the same plants at this location. The three species are, however, spatially segregated to some extent in that *T. ermineus* perches very near the top of large shrubs and small palo verde trees on the hilltop, *T. spatulatus* perches somewhat lower within many of these same plants, while *T. sculleni* perches very close to or on the ground about the outer edges of shrubs growing on the hilltop. Males of all three species tend to be site faithful with marked males returning to their perch sites over several days. In experiments in which resident males of *T. spatulatus* were removed, the replacements that arrived to occupy the trees tended to be smaller, suggesting that large body size confers an advantage in the defense of perching sites in this species. The mating system of these species can be labeled landmark territoriality, with males defending visually conspicuous sites on hilltops that presumably attract receptive females to the territory holders.

KEY WORDS: *Tachytes*, hilltopping behavior, mating system, Crabronidae, spatial segregation

The mating systems of wasps are highly diverse (Alcock *et al.*, 1978), a function of the fact that male mating tactics vary in relation to interspecific differences in the spatial distribution of receptive females (Emlen and Oring, 1977; Thornhill and Alcock, 1983). The most commonly documented mating system of crabronid wasps is one in which males patrol or perch within an area that serves both as a nesting location for adult females and an emergence site for receptive virgin females. When nests are clumped and numerous, there will be a season when many newly adult females are emerging from these nests within a relatively small area. Under these circumstances, males often engage in female defense polygyny, i.e., the direct defense of potential mates, with territorial individuals attempting to control access to emerging females. Alternatively, males of some species engage in scramble competition with their rivals by trying to find and outrace competitors to the virgins as they appear.

In addition to these two mating systems, males of some crabronids seek mates at resources, especially flowers, which attract receptive females, employing tactics that lead to resource-based polygyny. Finally, there are those crabronid wasps whose males perch on conspicuous landmarks of various sorts that attract widely scattered receptive females. These females probably are hard to locate as they emerge or as they visit resource-containing sites. Males of these species appear to be practicing a form of lek polygyny in which females choose males on the basis of their ability to defend territories that do not contain anything of utility to females (other than a potential mate) (Emlen and Oring, 1977; Thornhill and Alcock, 1983).

To date, the mating systems of only four members of the crabronid genus *Tachytes* have been studied. In all these species, males perch within the nesting/emergence

area, apparently waiting for receptive females to burrow their way out of the ground (Alcock, 1975; Lin and Michener, 1972; Kurczewski and Kurczewski, 1984; Elliott and Elliott, 1992). Males at these emergence sites have been observed defending areas around their perches by pursuing and even grappling with fellow males, leading to the conclusion that the males are territorial. If so, these species can be said to exhibit female defense polygyny, assuming that some territorial males mate more than once.

Here I report on male behavior in three species of *Tachytes* found at the same location, a mountaintop in central Arizona, at the same time of the year, namely late summer. I shall present evidence that males of all three species are engaged in "hilltopping territoriality" with individuals defending prominent landmarks at the tops of hills and mountains, presumably because these perch sites serve as visual markers that attract receptive females in search of a mate.

Materials and Methods

This study was conducted between 4 August and 19 September 2006 at the highest point within the Utery Mountains north of Mesa, Arizona. The study site consists of an undulating peaktop, which is sparsely covered with typical upland Sonoran Desert vegetation, including saguaro cactus (*Carnegiea gigantea* (Engelm.) Britton & Rose) (Cactaceae), foothills palo verde (*Parkinsonia microphyllum* Torr.) (Fabaceae), creosote bush (*Larrea tridentata* (D.C.) Cov.) (Zygophyllaceae) and jojoba (*Simmondsia chinensis* (Link) C. Schneid.) (Buxaceae). Further details on the area are provided by Alcock (1979).

During previous studies a 175 m transect path has been established along the peak ridgeline, which is where a number of palo verde trees, creosotes and jojoba bushes grow. After determining on 4 August that certain of these ridgeline trees and shrubs were being used as perch sites by male crabronid wasps, I made 25 additional visits to Utery Peak, spending between 90 and 150 min on the ridgeline per visit. The starting time for each visit varied, some beginning in the early morning, others at midday and still others in midafternoon.

I first tentatively established that there were three different behavioral and morphological phenotypes represented among the male wasps perching on trees and shrubs on the peak. (The three phenotypes varied in the height of their perch sites as well as in their abdominal coloration and size.) Thereafter, I began to census the transect to record which ridgeline plants served as perch-and-wait platforms for the male wasps. All the prominent ridgeline trees and shrubs had been given a number during previous studies of other hilltopping insects. When a perched male was located, an attempt was often made to capture and mark that individual with color dots on the thorax using a fine point paint pen (DecoColor® Paint Pens). Thereafter, records were kept of any resightings of this and all other marked males. Binoculars facilitated the identification of individuals so that they did not have to be recaptured in an insect net.

The height of perches used by the wasps on 1 and 2 September was measured using a 180 cm aluminum rod that was marked along its length at 30 cm intervals. The number of flights out and back from a perch during 2-min intervals (timed with a stopwatch) was recorded for individuals chosen haphazardly over the course of the study.



Fig. 1. A marked male of *Tachytes ermineus* perched on a leaf on the top of a jojoba bush regularly occupied by males of this species.

Males of *T. spatulatus* W. Fox that occupied regularly defended palo verde trees upon my arrival at the plants were considered “resident males.” Between 1 and 10 September, I removed 12 such residents and placed them in vials in a cooler. I then monitored the site for at least 1 hr and attempted to capture any male of *T. spatulatus* that came to the tree and began to perch there. These “replacement males” were captured, if possible, and were put in vials and eventually taken to my home where they and the previously captured residents were killed by freezing. I removed the specimens after an hour or so from the freezer and immediately weighed them to within 0.01 g on an Ohaus Portable Scale. The specimens were then pinned, labeled, and sent to Dr. Wojciech J. Pulawski who supplied a species name for each specimen. These voucher specimens and those of *T. ermineus* Banks and *T. sculleni* R. Bohart have been deposited at the California Academy of Sciences, San Francisco.

All statistical analyses were performed with the Quattro Pro program; means are presented ± 1 SD.

Results

Male Behavior In *Tachytes ermineus*

Between 4 August and 19 September, males of *T. ermineus* (Fig. 1) perched in a total of 16 trees and shrubs (12 palo verdes, 3 creosote bushes, and 1 jojoba) distributed along the ridgeline transect. Males were present in these plants from as

early as 0830 to as late as 1800 M.S.T. Males generally chose perches near the top center of the tree or shrub, with perch heights ranging from 75 cm in the smallest occupied shrub to 3.7 m in the tallest palo verde (mean perch height = 206 ± 92 cm, n = one measurement each from 15 plants).

From their perches, males sallied out to pursue passing insects, including conspecifics, or simply to shift perches. On a handful of occasions, the pursuer was seen to capture an apparent conspecific in flight and hold that wasp for a second or two in midair before the pair separated. Although these interactions happened too quickly to ascertain the sex of the participants, the rapid release of one wasp by another suggests that both individuals were males. For a sample of 19 marked wasps, the mean number of flights per minute was 4.3 ± 3.3 .

Males of *T. ermineus* exhibited considerable site fidelity. Nineteen (50%) of the 38 marked males were seen again on one or more days after the day of capture and marking. The mean number of days on which resighted males were seen was 3.9 ± 2.1 , during which time males occupied a mean of 1.3 ± 0.6 perch plants (14 of the 19 males were seen at only one shrub or tree). The mean interval from first to last sighting for these 19 males was 5.5 ± 4.6 days with a maximum of 15 days for two individuals.

Although only one male of *T. ermineus* occupied a given plant at a given moment, there were a substantial number of males in the area ready to occupy a site should it become available. For example, on 27 August, ten such replacements were captured between 0930 and 1030 after the removal of the marked resident male from a creosote plant growing on a high point on the ridge.

Male Behavior In *Tachytes spatulatus*

Between 4 August and 19 September, males of *T. spatulatus* perched in a total of 13 trees and shrubs (10 palo verdes, 2 creosote bushes, and 1 jojoba) distributed along the transect. Every tree or shrub occupied by *T. spatulatus* was also used at times as a perch site by males of *T. ermineus*. Some plants were more often occupied than others over the 19 daily censuses of the ridgeline. The correlation in the frequency of occupation of all 16 sites by the two species was 0.29 ($P = 0.25$, d.f. = 15). This statistically insignificant result reflects the rarity with which males of *T. spatulatus* perched in the several smaller shrubs favored by males of *T. ermineus*. If we consider only data on the occupation of the 12 much larger palo verde trees chosen by the two wasp species, the correlation between their perch preferences increases: $r = 0.55$, d.f. = 11, $P = 0.052$. This statistically borderline result suggests that the palo verdes used as perch sites were assessed similarly by males of the two species.

The daily period of activity ranged from 0900 to as late as 1700. During this time males of *T. spatulatus* perched near the top of the selected tree or shrub and in the center of the plant, with perch heights ranging from 60 cm to 2.75 m (mean perch height = 204 ± 60 cm, n = 10 measured sites). On August 9, when a male of *T. spatulatus* shared a tree or shrub with a male of *T. ermineus* at ten different sites, all the males of *T. spatulatus* were perched lower in the plant than their congener ($P < 0.01$, sign test) with a mean difference of 40 ± 24 cm between the heights of the two perches.

As was true for *T. ermineus*, males of *T. spatulatus* made regular forays out from their perches. For a sample of ten wasps, the mean number of flights per minute was

2.3 ± 1.9 . When a plant was occupied by males of the two morphologically distinct species, the two residents occasionally interacted with one wasp pursuing the other rather slowly before each returned to his respective perch.

Males of *T. spatulatus* were also site faithful as a rule. Seventeen (57%) of 30 marked males were observed on one or more days after the day of capture and marking. The mean number of days on which resighted males were seen was 2.9 ± 1.2 , during which time males occupied a mean of 1.2 ± 0.4 perch plants (13 of the 17 resighted males returned to one shrub or tree). The mean interval between first and last sighting for the 17 resighted males was 3.8 ± 1.4 days with a maximum of 6 days, doubtless an underestimate given that I collected several of the 17 marked individuals for the purposes of identification, thereby shortening the territorial tenure of these males.

As was true for *T. ermineus*, there were potential competitors for suitable perching plants. Between 1 to 10 September, males of *T. spatulatus* were removed from a total of 8 plants on at least one occasion; from one to four replacements appeared at five of these plants within 2 hr of the resident's removal.

If, as seemed likely, residents were preventing others from perching in their tree or shrub, then replacement males could be predicted to be smaller than their rivals, given the near universal advantage enjoyed by larger males in the competition for mates (Blanckenhorn, 2000). This rule applies to another species of *Tachytes* in which there are large territorial and smaller nonterritorial males (Elliott and Elliott, 1992).

Size variation among males was evident in *T. spatulatus*, and as predicted, the mean weight of first captured replacements (0.066 ± 0.018 g) was significantly less than the mean weight of 12 removed residents (0.081 ± 0.011 g); matched pair *t*-test $t = 2.57$, $P < 0.03$.

Three replacement males proved to be ex-residents that had been marked at the site earlier in the study. A comparison of the mean weight of all current and ex-residents ($n = 15$) versus the mean for all 20 unmarked replacement males, including second, third and fourth replacements, reveals a highly significant difference in weight between the two groups: (0.083 ± 0.010 g for the residents versus 0.062 ± 0.016 g for the replacements; $t = 4.34$, $P < 0.001$).

Male Behavior In *Tachytes sculleni*

This wasp was the least abundant *Tachytes* on the hilltop. Three males were collected and kept when first seen while six others were captured, marked, released and observed between 14 August and 2 September. The daily period of flight activity began as early as 0945 and lasted as late as 1705.

The nine males of *T. sculleni* were found on only three shrubs (two jojobas and one creosote bush) scattered at substantial intervals along the ridge. The creosote bush and one of the two jojobas selected by this species were also regularly occupied by *T. ermineus* with very occasional visits from males of *T. spatulatus* as well (although these two species perched much higher within the shrubs they occupied with *T. sculleni*). The jojoba that was utilized only by males of *T. sculleni* was situated within a few meters of palo verde # 2, the most prominent landmark along the ridge and a highly favored perch site for the other two species (Fig. 2).

In contrast to males of *T. ermineus* and *T. spatulatus*, males of *T. sculleni* usually perched very close to the ground (and never more than 43 cm high) on the outer edge

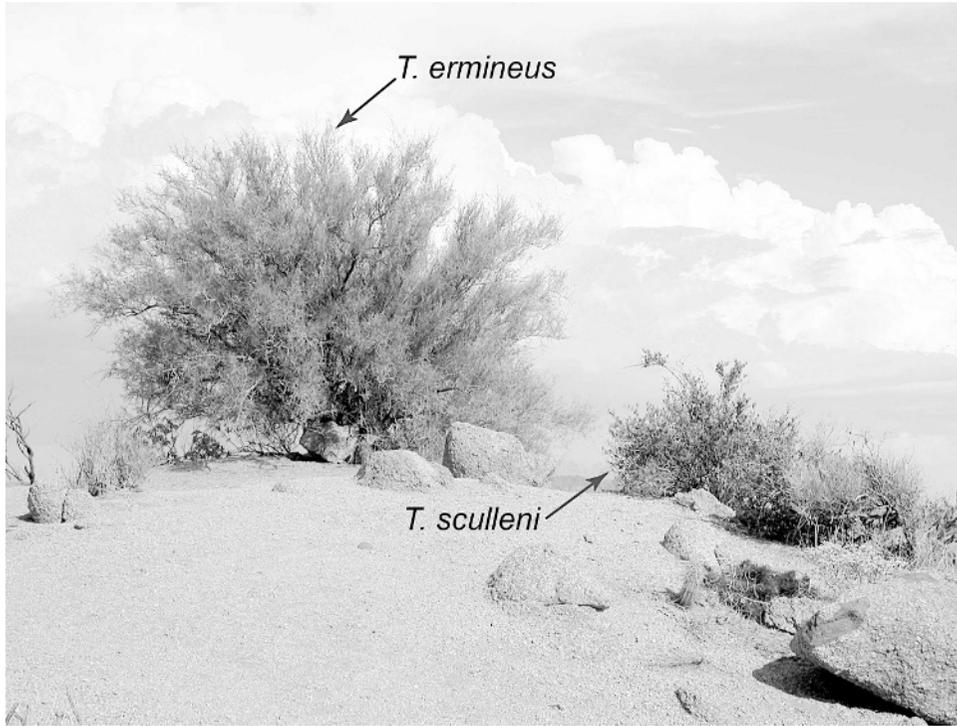


Fig. 2. Spatial separation of *Tachytes* perching sites on Usery Peak. Males of *T. ermineus* perched high in the central portion of palo verde # 2, while males of *T. spatulatus* perched below them. Males of *T. sculleni* occupied the lower outer edge of the jojoba bush shown here.

of the chosen shrubs rather than in the center. Some individuals even rested on the ground itself so that the average perch height was 20.6 ± 15.3 cm ($n = 6$ marked males in the three selected shrubs). From these perches, males launched occasional flights, generally returning to the same or nearby resting sites. On one occasion, two wasps believed to belong to this species were observed in an apparent chase involving rapid low circling flight over the ground near the perch site of one of the contestants. Only one male returned from the chase. Four of the six marked individuals of this species demonstrated site fidelity in that they were observed at the spot where they had been marked on at least one other day.

Discussion

Male behavior in *Tachytes ermineus*, *T. spatulatus*, and *T. sculleni* appears to be highly similar. In all three species, males perched for many hours each day on twigs, leaves or branches of trees and shrubs growing at the top of a mountain in central Arizona. From their perches, males launched brief out-and-back flights to pursue passing insects and perhaps also to patrol the tree or shrub in which they were perching. Only one male of a given species occupied a selected hilltop tree or shrub at any time, although the same plants often simultaneously accommodated males of both *T. ermineus* and *T. spatulatus*. Removal of a current resident of *T. ermineus* and *T. spatulatus* often resulted in its quick replacement by another conspecific,

indicating that males defend their perching plant against rivals, i.e., these males are territorial. Moreover, a fairly high proportion of males of all three species exhibited site fidelity by returning on subsequent days to the plant where they were originally captured and marked. The territoriality hypothesis is also supported by the finding that resident males of *T. spatulatus* tended to be larger than their replacements.

These attributes are characteristic of territorial, hilltopping insects (Shields, 1967; Alcock, 1987). Males of these insects attempt to monopolize conspicuous perch lookouts on hilltops where they wait for receptive females to fly to them. Upon the arrival of a female at a landmark plant, the territory owner attempts to mate with her. Examples of this mating system are fairly common in the Lepidoptera, Diptera, and Hymenoptera. However, the only crabronid wasp previously reported as a hilltopper is *Bembix furcata* Erichson, whose males patrol hilltops in Queensland, Australia (Dodson and Yeates, 1989). The site-faithful patrollers chased intruder males from the area. The absence of nesting, emerging, or foraging females of *B. furcata* at this location led Dodson and Yeates (1989) to suggest that males were engaged in landmark-based territoriality rather than female- or resource-based territoriality.

Likewise, the absence on Userly Peak of nesting, emerging, or foraging females of the three species of *Tachytes* suggests that males of all these wasps also engage in landmark-based territoriality. Indeed, during the current study, no females of any of the *Tachytes* wasps were seen, a not uncommon occurrence in studies of hilltopping insects. In these species, males typically greatly outnumber receptive females at the hilltop, thanks to the many hours each day that males invest in territorial defense of their perch sites. In contrast, females generally appear on ridgetops just long enough to mate before going elsewhere to forage and oviposit. Thus, for example, despite many hundreds of hours of observation distributed over 10 spring field seasons in the Userly Mountains, only 33 matings have been recorded for the pompilid wasp, *Hemipepsis ustulata* Stål (Alcock and Kemp, 2006), another territorial hilltopping wasp whose males have at various times defended all 17 of the plants used as perch sites by the three species of *Tachytes* wasps.

One of the more unusual features of the hilltopping behavior of the *Tachytes* in this study was the co-occurrence of three congeneric species whose males overlapped substantially in the timing of their activity and in the selection of perch sites. In central Arizona, most hilltopping species are represented by a single member of a given genus, although among the butterflies, two species of *Chlosyne* and four species of *Vanessa* can sometimes be found on the same high points at the same time of day (Brown and Alcock, 1991; Alcock, pers. obs.). Moreover, Jiggins (2002) reports finding up to 16 species of *Acraea* butterflies on an Ugandan hilltop. Given the low threshold for sexual and aggressive pursuits by hilltopping males, the cost of hilltopping territoriality could rise when congeners occupy the same sites because of the time and energy wasted by males when they chase similar-looking heterospecifics. Indeed, males of *T. ermineus* and *T. spatulatus* often interacted when they perched in the same palo verde or creosote bush. The benefits of reducing fruitless interactions of this sort may be responsible for the fact that *T. ermineus* consistently perched higher than *T. spatulatus* while *T. sculleni* perched far below the other two. Alternatively, a female preference for ease in locating conspecifics while avoiding congeneric males may have supplied the selection pressure responsible for the spatial segregation exhibited by the male *Tachytes* in this study.

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