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ADDITIONAL OBSERVATIONS ON *TACHYPOMPILUS FERRUGINEUS* WITH EMPHASIS ON MALE BEHAVIOR (HYMENOPTERA: POMPILIDAE)

Frank E. Kurczewski¹

ABSTRACT

An aggregation of 11 males and 5 females of *Tachypompilus ferrugineus* was studied during August and September 1989 at a 2 m-high cemetery monument in Syracuse, NY. Male perching behavior and male-male and male-female interactions are described. Male-male interactions included acceptance, perching in close proximity, wing fanning, circling, following, and flight chases. Overt territoriality was not demonstrated by individual males, although several wasps each maintained a few or several stations. Despite noticeable size variation among wasps, there was no dominant-subordinate hierarchy. Male attachment to the cemetery monument waned as the season progressed due to mortality, increased floral feeding, and decreased female receptivity. Several males often simultaneously pursued an incoming female in an attempt to mate and such males exhibited extensive wing fanning and antennal waving.

In 1989 I presented the first observations on the ecology, mating, and nesting behavior of *Tachypompilus ferrugineus nigrescens* (Banks), a melanic color form that occurs in the northeastern United States. The observations were based upon a study made during mid-summer 1988 at a cemetery monument in Syracuse, NY. These observations led me to conclude that there is no biological validity for separating this subspecies from the more erythritic *T. f. ferrugineus* (Say). During the summer of 1989, I had the opportunity to study the progeny of this aggregation primarily from the standpoint of male activity and behavior rather than female nesting behavior. The results of this study, one of the few on male behavior in pompilids, are presented below.

MALE BEHAVIOR

Males were observed on 1–31 August 1989 between 0950 and 1435 h (EDT) at ambient temperatures of from 19° to 34° C at the same site as described in 1989. They had emerged later in 1989 than in the previous summer (23 July 1988) due to a delayed spring and atypical rainfall pattern and, consequently, their flight season occurred later in the year. As many as 11 males perched simultaneously on the cemetery monument on 4 August 1989; this number was reduced to eight by 10

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August and then to five by 15 August. Only three males occupied perches there from 18–23 August and, by 25 August, only a single male was in evidence.

Males perched on the pedestal of the monument in the shaded (E) side in an area 57 cm long and 33 cm wide, 9–42 cm above ground level, except for one wasp that stationed himself on a pile of leaf litter just below an opening in the crevice in which the females were nesting. Six males perched together on 4 August in an area 23 cm long; two pairs of such males perched as close together as 0.6–0.8 cm, often in a head-beside-head attitude, without showing any visible sign of reaction to crowding. A perched male appeared to be alert or ready, as indicated by his slightly raised antennae, outstretched but raised legs and raised body, as opposed to a resting male with legs and antennae outstretched but lowered and body flattened against the stone.

Eleven males perched head downward toward the ground 201 times, following 223 landings on 4 August; these wasps perched head upward only 8 times and head sideways 14 times. Perching following landing by eight males on 10 August revealed similar attitudes: 30 head downward; 4 head upward; 2 head sideways. The head downward perching attitude became less rigid as the season progressed, as exemplified by three males on 21 August: 34, head downward; 12, head upward; 11, head sideways.

Overt territoriality, such as fighting, grappling, instantaneous chasing, or usurpation, was not demonstrated by any of the males. Five of them perched repeatedly on the same protuberances or other raised spots on the pedestal, indicating that some males had preferred stations. Three males returned to their previous perching sites on successive landings. One wasp perched at intervals of 4–28 min on a pile of leaf litter near an opening into the basal crevice (see Kurczewski, 1989) and he returned repeatedly to this site between 4–18 August. He also maintained a few other perches on the pedestal of the monument.

As a male approached the monument in flight, he invariably kept his head oriented toward the stone. Upon landing, he flicked or waved his wings a few times and then held them still but raised at a 35–45° angle for 1–3 sec, as in species of *Episyron* and *Poecilopompilus*, before lowering them flat on the dorsum. This was followed occasionally by rubbing the hindlegs over the back half of the wings and then rubbing the hindlegs together, or cleaning the antennae with the strigili of the forelegs.

Early in the season (1–15 August), males approaching the monument in flight evoked little or no response from males perched on the stone if they landed further away than ± 1.0 cm. A resident male often accepted an intruding one and the two maintained perches sometimes only 0.6–1.5 cm apart. If, however, an incoming male landed near (± 1.0 cm) a perched male, the two interacted almost immediately. The perched male usually turned, pivoted, or moved sideways to meet the intruder head on or sideways. In 3/4 of male-male close proximity interactions, the resident walked toward the intruder and the two circled one another in a clockwise or counter-clockwise manner, or the resident followed behind the intruder as the latter walked away. Such following of one male by another lasted only 1–2 sec. Sometimes, while circling, the resident male or both males mildly fanned the wings but not overtly so as in the case of a male-female interaction. In 1/4 of the interactions, circling culminated with the resident male chasing the intruder from the monument in a twisting flight which, in turn, often evoked a series of in-tandem flight chases from other males perched nearby. The chasing of one male by another increased per number of interactions as the season progressed and females became less receptive. Late in the season (18–23 August) there was a flurry of flight activity around the monument as resident males landed and took off or chased intruders in flights 2–4 m high.

Despite noticeable variation in the sizes of the males (body lengths, 11–15 mm), there was no visible size-related dominance exhibited by the wasps. Small males followed and chased large males 37 times and vice versa, 39 times. Body size of

males was not correlated with clockwise or counter-clockwise circling behavior. Small and large males circled one another in both directions. Small males maintained 34 perches near the basal crevice in which the females nested and large males, 31 perches. One large male (body length, 15 mm) lived +21 days while a small male (body length, 12 mm) lived +23 days. Three different-sized males appeared equally early in the day to maintain perches on the monument; two smaller males appeared at 1041 and 1045 while one larger one made his appearance at 1052 on 18 August.

The number of males seen at the monument decreased from 11 to 1 and they spent increasingly less time there from 1 to 31 August. Male mortality, increased feeding by males at *Daucus carota*, and apparent female unreceptivity are probable reasons for this diminished male activity. Following wasp emergence (1 August), during which males appeared 1-2 days before females, both sexes spent a considerable amount of time at or near the monument. On 4 August (ambient temperature, 34° C) 11 males spent 47 percent of their time at the monument; of this time, 93 percent was spent perching and only 7 percent, walking or flying nearby. On 10 August (25.5° C) seven males spent equal amounts of time perching or walking and flying nearby. On 22 August (22° C), three males continuously landed, perched for 30 sec-1 min, flew away, returned 5-17 min later, perched briefly, etc. During a 30 min-period on 23 August (23° C), three males spent a total of only 6.5 min perched on the monument or walking thereon and 83.5 min elsewhere. Upon leaving, such males flew upward, facing the monument, circled it one or more times, and then made a direct but sinuous flight toward a stand of *D. carota*. Finally, on 28-31 August (21.5°-25.5° C), the last male to be seen flew to the monument at 5-18 min intervals, circled the monument but never landed, flew to other monuments and circled them but did not land thereon.

MALE-FEMALE INTERACTIONS

All male-female interactions observed took place on the pedestal of the monument. Early in the season (1-10 August), males pursued females as the latter landed and entered the basal crevice to nest. Males appeared at the monument earlier in the morning (0950-1040) than the females (1020-1115) and perched near the crevice. A female usually landed on the lawn several minutes after the males had appeared and walked onto the pedestal of the monument, flicking her wings incessantly, at which time one or more males approached her face to face or from the side and began waving their antennae and fanning their wings and possibly producing a sound therewith. Unmated females usually fanned their wings and waved their antennae in response to the male wing fanning and antennal waving, and mating ensued shortly thereafter (see Kurczewski, 1989). Mated (nesting) females were reluctant to copulate but were trailed, often by three or four wing-fanning and antennal-waving males, as they ran into the basal crevice. Other males in the vicinity flew around the female erratically as she ran across the pedestal. Males did not follow females into the crevice. On 4 August, four males trailed and five others flew around a single female as she attempted to enter the crevice. After this female had entered, three males continued to run on her trail, fanning their wings and antennating the area of the pedestal over which she had run. This activity totally disrupted the perching of all 11 males and they eventually flew away after a flurry of flight activity. After 10 min, only one of the males had returned to the pedestal to resume perching at a station.

FEMALE BEHAVIOR

In 1988 females nested within the basal crevice on the W side of the monument which was in sunshine for much of the day (Kurczewski, 1989). In 1989, two females

constructed nests within this crevice on the E and N sides of the monument in a mostly shaded situation. Another wasp enlarged a portion of the crevice on the S side by removing earth and debris to the outside. A fourth wasp nested in an earthen crack in the soil beneath an adjacent smaller tombstone. This female was seen to take inside a piece of dried oak leaf, 0.9 x 1.3 cm, possibly for use as fill.

As in 1988, females returned periodically (9–45 min) to the monument, entered the crevice, sometimes on one side, and exited frequently from another side. Such wasps remained within the crevice for from 1–13 (\bar{x} = 8) min; they then usually flew away in a rather straight line, after walking a short distance, and recommenced hunting for prey or, twice, took nectar from the flowers of *D. carota*. Such periodic returns probably served as reorientation to the hunting wasp.

Females hunted for Lycosidae in leaf litter and inside earthen cracks and depressions, 4 m N and 6.5 m W of the monument, from 10 August to 5 September 1989 at ambient temperatures of 22°–33° C. Hunting on the ground surface involved extensive wing flicking, antennation of the substrate, and periodic flights to new hunting areas. One wasp landed on an *Agelenopsis* (Agelenidae) web, ran on it with wings outstretched at about a 45° angle but not flicking upward, and then flew away hurriedly. The occupant of the web was missing.

The prey of one wasp, a *Lycosa rabida* (Walckenaer) (Lycosidae) female, weighing 641 mg, recovered from the effects of the venom and walked away from the depression in which it had been placed.

DISCUSSION

Until rather recently, virtually nothing was known about male behavior in the Pompilidae (Krombein, 1979). Richards and Hamm (1939), Evans (1948), and Evans et al. (1953) noted flight activity of male pompilids and brief encounters between males and conspecific females. Wasbauer (1955, 1957) described several unsuccessful mating attempts by male pompilids in the genus *Anoplius*. He observed that several males often pursued a single female of *A. fulgidus* Cresson and that they became "greatly agitated" when in the vicinity of a female. Barrows (1978) reported patrolling flights and mating attempts of *Evagetes subangulatus* (Banks), a cleptoparasitic spider wasp. He noted that the males did not establish well-defined territories nor did they perch repeatedly on particular landmarks.

In a series of monumental studies, Alcock (1978, 1979, 1981) established that males of the tarantula hawk *Hemipepsis ustulata* Dahlbom defended territories in treetops located high on mountainous ridges. Territory owners were usually larger than conspecific non-territorial visitors. The largest resident males occupied territories closest to the peak of the mountain; smaller males were intruders in these areas or established territories below the preferred mountaintop ones.

In the present study, males of *Tachypompilus ferrugineus* maintained a loose network of stations or perches on an upright cemetery monument but they did not defend these sites vigorously against one another. Lack of overt territoriality in this species may be related to centralization of all activity, both male and female, on an obvious visual landmark, i.e., the cemetery monument. Acceptance rather than aggression was the rule during encounters between conspecific males until midway through the nesting season. Increased aggression between males as the nesting season progressed may be linked to female unreceptivity and their preoccupation with nesting activities. Male station maintenance, i.e., perching, became less rigid with increased female nesting activity and presumed female unreceptivity. Toward the end of the nesting cycle, only a few males were observed perching on the cemetery monument although male mortality may have been the primary reason for this lack of activity.

Early in the nesting season, practically all males of *T. ferrugineus* perched head downward facing the crevice of the monument in which the females nested. As the

number of nesting females increased and they became increasingly unreceptive to male advances, the head downward posture of the males perching on the monument became less rigid, i.e., more males perched in head upward and head sideways attitudes. Males spent increasingly less time in the perched position and more time walking, flying, or obtaining nectar from the flowers of *Daucus carota*.

Shortly after emergence, when nearly a dozen males of *T. ferrugineus* each maintained a few or several stations on the monument, male activity focused on females flying in, landing, and walking into the crevice. Several males usually pursued a single female, waving their antennae and fanning their wings rapidly and possibly thereby producing a sound. Apparently receptive unmated females signalled back to an approaching male with their antennae and wings as they stood face to face or side by side, and mating ensued shortly thereafter with the smaller male positioned atop the larger female (see Kurczewski, 1989). Apparently mated nesting females were reluctant to mate, paid little or no attention to the displaying males, and entered the crevice without hesitation.

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