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TERRITORIAL BEHAVIOUR BY MALES OF *PHILANTHUS MULTIMACULATUS* (HYMENOPTERA: SPHECIDAE) WITH A REVIEW OF TERRITORIALITY IN MALE SPHECIDS

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Abstract. Males of *Philanthus multimaculatus* Cameron defended a perch site near a nesting aggregation against other conspecific males. Vigorous aerial clashes between a resident and an intruder were common, with the resident male ejecting the invader in the vast majority (84 per cent) of cases. One copulation was observed at the perch thus supporting the hypothesis that territoriality was related to securing a favourable location for mating. Male reproductive strategies in the Sphecidae are reviewed; territoriality appears to occur in this group when (1) receptive females are clumped in space, (2) there are cues that permit males to identify superior localities for reproduction, and (3) these locations are small enough to be relatively easily defended.

The behaviour of male digger wasps has attracted relatively little attention. However, there are a number of useful studies including Lin's (1963) paper of male territorial behaviour in the cicada killer, Kurczewski's (1966) study of male behaviour in the genus *Tachysphex*, and a comparative investigation of *Oxybelus* (Peckham, Kurczewski & Peckham 1973) that provides a great deal of interesting information on male activities. The present paper deals with the behaviour of male *Philanthus multimaculatus* with special emphasis on territoriality.

Territorial behaviour, defined as the defence of an area, has not been reported for many insect species (Brown & Orians 1970). Nevertheless, the behaviour has been observed in at least five genera of sphecid wasps (for reviews see Lin 1963, Evans 1966a and Kurczewski 1966). The literature on *Philanthus* (reviewed by Alcock 1974) contains few references to male activities and almost no mention of territoriality with the important exception of a paper on *P. triangulum*, the European bee-wolf (Simon Thómas & Poorter 1972). Some males of *P. triangulum* vigorously defend a territorial station around small pine trees; these males tend to occupy the same location for many days, skirmishing with intruding males and mating with visiting females. Males of *P. multimaculatus* also engage in elaborate aggressive bouts as they seek to claim or defend a perch. This paper describes the behaviour of territorial males and their opponents as well as discussing male reproductive strategies in the Sphecidae.

Methods

This study was conducted from 18 to 28 July 1973 in Portal, Arizona, on a low ridge bordering Cave Creek, located about 1 km north on the road to San Simon. The general area and its flora have been described by Linsley & Cazier (1972). The ridge was fairly open with only scattered patches of vegetation and dried clumps of peppergrass (*Lepidium montanum*). The area was fully exposed to the sun with air temperatures reaching 30 to 35°C by mid-day. One patch of peppergrass about 30 × 20 cm in area with dried leafless stems reaching some 20 cm in height was the focus of activity for a number of male *P. multimaculatus*. At least one male came to the weed and remained there for some time on every morning during the study with the exception of 22 July. I was present at the site each morning for 1 to 5 hr and recorded 15 hr of observations of one or more males at the peppergrass clump. (The wasps could be sexed easily because the first yellow abdominal band of the male was unbroken, whereas this band was split by a conspicuous black bar in the female.) To identify individuals, four territorial males were given a dot of red acrylic paint on their thorax.

Results

Daily Pattern of Activity

Males exited from sleeping burrows between 09.00 and 10.00 hours as a general rule. One male constructed a 4-cm-long tunnel that extended horizontally into the side of a small depression and used this burrow repeatedly as a sleeping place. Other males entered females' nests in the late afternoon and spent the night there (a pair was found together in a burrow as I excavated the nest in the early morning).

After emerging, males groomed themselves and visited flowers. Sometime between 09.07

and 10.08 hours a male would arrive at the peppergrass perch; males remained at the site until 09.50 to 12.35 hours (eight records). No individuals were seen at this location after 12.35 hours, although I often inspected the area in the afternoon. Lin (1963) also observed that the number of male *Sphecius speciosus* defending territories fell sharply in the afternoon. However, *P. triangulum* males are most active territorially in the afternoon in France (Simon Thómas & Poorter 1972).

Behaviour at the Perch

The behaviour of the eight or more males that came to the perch was highly similar. Upon landing on the peppergrass a male would first walk a short distance (2 to 10 cm) holding its body in a shallow inverted V so that its head and the tip of its abdomen touched the stem (Fig. 1). It is possible that this position is associated with the deposition of a pheromone (from either mandibular or abdominal glands) designed to induce females to approach and land in the plant (see below). The male then might stop, often in a 'head-down' position (Plate XVI, Fig. 2). Sooner or later the male would fly a short distance out and then back to the plant, always orienting its body into the wind (generally light to moderate at the site). Upon landing, the insect would repeat the pattern of walking and then stopping or sailing out on another short flight (Fig. 3). Somewhat similar behaviour has been observed in *P. triangulum* (Simon Thómas & Poorter 1972) and *P. crabroniformis* (Alcock 1974).

When a male had just arrived on territory flight activity was frequent, but the longer he remained the fewer flights he took per unit of time (Fig. 4). The decrease in flights was not due simply to an increase in temperature as the morning progressed. The correlation between the number of flights in a 5-min period and the time of day was not significant ($r = -0{\cdot}42$; $P > 0{\cdot}10$). The inverse correlation between flights per 5-min period and the amount of time since the male's arrival at the perch was highly significant ($r = -0{\cdot}85$; $P < 0{\cdot}01$).

During 15 hr of observing a male on the perch, only one copulation occurred. In fact, females were almost never seen in the vicinity of the peppergrass site although it was only 3 m from a nesting aggregation of five to ten wasps. On 24 July at 10.51 hours a female flew slowly upwind and alighted on a stem that was bent parallel to the ground. The male, having left his perch on the approach of the other wasp, almost immediately dropped down onto her back facing in the same direction as his mate. Coupling was achieved in a matter of seconds. The male soon dismounted and moved to the side of the female while clinging to the stem. The bodies of the copulating pair formed a narrow V. This position is atypical of the Sphecidae as a whole (Lin 1966, 1967) which normally employ a male above–female below pattern throughout copulation. However, males of *P. triangulum* (Simon Thómas & Poorter 1972) and *P. crabroniformis* (Alcock 1974) also dismount during mating as do males of another philanthine wasp, *Cerceris frontata* (Scullen 1965), suggesting that the behaviour may be widespread in this subfamily. The duration of copulation was 5 min. The pair shifted position slightly before uncoupling; the male then flew up and landed again on the female's back, but this time she flew away.

Male–Male Interactions

Fifty-three encounters between a perched male and an 'intruder' or 'intruders' were seen in 15 hr of observation. These clashes had the effect of driving all but one of the intruding males away. On only three occasions were two males present at the perch site together (for 9, 13, and 26 min respectively). In each instance, one male was active, flying out repeatedly from the plant while the other remained perched, usually on the outer part of the weed away from the area frequented by the active male. The second male appeared to retain its perch only because it did not attract the attention of its rival. Males interacting with one another employed the following behaviour patterns:

(a) Strike and flee: Intruders sometimes approached perched males and struck them by dropping onto their back. The visitors then immediately flew off.

(b) Hover–orient: Male residents left their perch after having been struck or on the approach of another male and oriented toward the intruder while hovering. In the course of an

Fig. 1. A sketch of a male dragging the tip of its abdomen and its mouthparts along a stem of a peppergrass plant. Drawn from a photograph.

PLATE XVI

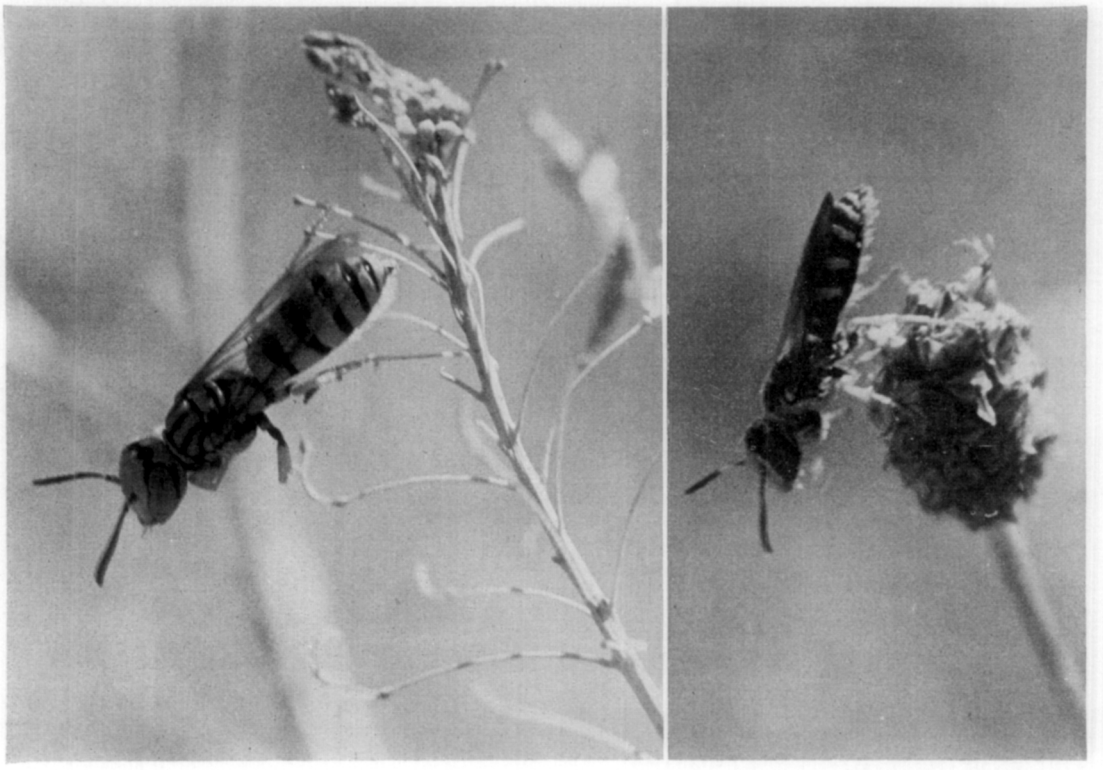

Fig. 2. (Left) A male *P. multimaculatus* in the head-down scanning position. (Right) A male *P. crabroniformis* in the same pose. Note that in both species the head is slightly raised and the front legs are drawn up under the male's chin.

aggressive bout the intruder sometimes hover-oriented toward its opponent.

(c) Darting flight: Following a hover-orient, males often flew rapidly at the side of their rival, but contacts were rare.

(d) Swirling flight: Frequently a pair flew side-by-side in circles and loops with such speed that it was difficult to follow them.

(e) Vertical flight: A male might fly slowly upward with the other wasp trailing under and slightly behind it at a distance of 2 to 4 cm.

(f) Drop–strike: The higher of the two males in vertical flight almost always dropped onto the back of the other male before reaching a height of 50 cm. The drop–strike usually resulted in only a momentary clashing of wings and bodies, but sometimes one or both males were driven to the ground by the collision.

(g) Grappling: On two occasions only, males fell to the ground together and grappled with one another for a few seconds before flying up again.

(h) Pursuit flight: Many times it was clear that one wasp was fleeing from the area with its opponent in pursuit. Unlike swirling flight when the two males flew side-by-side, in pursuit flight one male went straight off with the other directly behind it. Pursuit flight generally terminated a skirmish.

These behaviour patterns occurred in a majority of all encounters with the exception of (a) and (g). Simon Thómas & Poorter (1972) report various chase fights for *P. triangulum* as well as something approximating 'vertical flight'. However, they never saw two males make contact with one another.

Wasps that retained or gained exclusive rights to the perch can be considered winners of an encounter. Because of great individual differences in size and coloration of males (some were 3 mm longer than others, some were very yellow, others yellow-green), it often was possible to determine with some certainty whether the winner was the resident male or whether the intruder had won. In addition, having marked four males, I was able to be absolutely certain of the identity of the winner in some cases. As is customary in territorial matters, the resident male succeeded in repelling its opponent in the vast majority of disputes (Table I). It was my subjective impression that when an intruder won it was larger than the resident with only one exception.

Site Tenacity

Although the perch area always was defended when a male was present, the ownership of the site changed hands frequently as a male came and then left of its own volition after an average stay of 78 min ($N = 7$) or was driven off by an intruder after 37 min ($N = 4$). As many as three different males, and possibly more, claimed the perch during a single morning. Moreover, a male that appeared one day was not very likely to come to the weed again. Only one of four marked wasps was seen at the site on more than a single day (on 21, 23 to 27 July), and often the returnee was quickly driven away by the resident male of the moment. Therefore, there seems to have been a pool of wandering males, a fair number of which were drawn to one patch of peppergrass. Those that could claim the site defended it for an hour or so and then left not to return for several days at least.

Discussion

Brown & Orians (1970) note that territoriality in insects generally involves defence of an area advantageous for reproduction (altough territorial occupation of foraging areas is common among social insects, Wilson 1971). For example, the bee *Protoxaea gloriosa* guards a flowering plant attractive to virgin females of its species (Cazier & Linsley 1963). Males of the crabronine wasp *Oxybelus subulatus* defend one nest and mate repeatedly with the female that provisions it, while driving away all other insects (Peckham et al. 1973). Cicada killer males defend an area where there are many emergence holes, a sign of high nest density and therefore a cue that many virgin females eventually will appear in the area (females emerge after the males). The behaviour of *P. multimaculatus* appears to fit the general rule with males defending a location that is for

Table I. The Outcome of Male–Male Conflicts at the Perch Site

	Winner		
	Resident*	Intruder	Sign Test (P)
(A)	16	3	$< 0{\cdot}01$
(B)	16	2	$< 0{\cdot}01$

(A) = Resident and intruder easily distinguished on the basis of size and colour differences.
(B) = One or both combatants possessed a distinctive colour mark.
*A minimum of eight resident males.

some reason advantageous for mating. However, in one respect the territorial behaviour of this wasp is unusual. Generally territorial males, including *P. triangulum* (Simon Thómas & Poorter 1972), stake claim to an area and retain ownership of the spot for a substantial period of time. Males of *P. multimaculatus*, however, compete for a limited piece of real estate with ownership continually changing hands, a phenomenon that might be called serial territoriality.

This raises two questions for which I can provide only the most speculative of answers: What was so attractive about the perch site? Given its evident attractiveness, why did most males defend it for such a short time?

Males may have preferred this one clump of peppergrass because it was especially well-suited for scanning an area where females might be found. However, many other patches of the weed were available and appeared to be equally advantageous for this purpose; yet they were ignored. It is therefore at least possible that the attraction exerted by this particular site stemmed from an application of a pheromone. If males did employ an attractant pheromone it would help explain why males sought to defend this one area and why other males attempted to claim the spot despite the presence of many superficially similar clumps of peppergrass scattered along the ridge.

Second, in dealing with the failure of most marked males to return to the perch site, one must consider the possibility that capture and marking influenced their behaviour. However, in every case, the freshly-marked males flew to a nearby bush to groom for a brief period and then returned to defend the site once again. There may have been other perches unknown to me or male *P. multimaculatus* may have possessed a variety of strategies for reproducing, territorial defence of a favoured perch being only one of several options. More information is required to test these hypotheses.

I should like to draw attention to the wide range of behavioural strategies exhibited by male sphecids designed to lead to copulation. The diversity of adaptations, even within a single genus (e.g. *Oxybelus*, see below), is striking and raises questions about the ecological and evolutionary factors that ultimately are responsible for it. I list in Table II some different male activities, examples of species that practise these activities, and whether or not these species are known to be territorial.

This review, although dependent upon our very incomplete knowledge of male sphecid behaviour, does permit some tentative generalizations. As Brown & Orians (1970) have pointed out, the key question about territoriality is, under what conditions should selection favour increased or decreased aggressive behaviour with respect to space? If we assume that male sphecids act to maximize their fitness, when should it pay them to make a substantial time-and-energy investment in defending an exclusive preserve? Perhaps the key ecological factors are (1) the spatial distribution of females that can be mated, (2) the availability of cues that permit identification of an area where one or more receptive female is especially likely to appear, and (3) the defensibility of these locations. In

Table II. Sphecid Male Behaviour and Territoriality

Male Behaviour	Territoriality?
A. Males patrol a broad area in:	
(1) a nesting location	
Most nyssonine wasps: Evans 1966b;	No
Oxybelus bipunctatus: Peckham et. al. 1973	No
(2) a female hunting or feeding area*	?
B. Males wait at a perch (or limited number of perches) in:	
(1) a nesting location	
P. multimaculatus, Tachysphex terminatus: Kurczewski 1967; *S. speciosus:* Lin 1963;	Yes
Astata unicolor: Evans 1957;	Yes
Oxybelus emarginatus: Peckham et. al. 1973;	Yes
Stictia carolina: Evans 1966b	Yes
(2) a female hunting or feeding area*	?
C. Males hover:	
(1) near a sleeping site	
Steniola obliqua: Evans 1966b	No
(2) over a small portion of a nesting area	
Stictia vivida: Evans 1966b	Yes
D. Males wait by or inside a female's burrow:	
Oxybelus subulatus: Peckham et at. 1973;	Yes
O. sericeum: Bohart & Marsh 1960;	Yes
Tachysphex apicalis: Kurczewski 1966:	Yes
Trypoxylon spp.: See Evans 1966a	Yes

*Males of many species are known to mate with females at flowers. However, whether individuals take up residence at a particular flower or patch of flowers and wait there for a female or whether males patrol over a wide area visiting many different flowers in search of females does not appear to be well documented.

the Sphecidae territoriality appears to have evolved when (1) receptive females are highly clumped or when single receptive females appear predictably in one spot, (2) there are cues that permit males to identify superior locations for reproduction (i.e. areas where a receptive female is likely to appear), and (3) these locations are small enough to be readily defended. To take the most clear-cut case, territoriality apparently has evolved in all those species in which a male waits in a burrow and copulates with the female that constructed the nest. When a female's eggs are not all fertilized with sperm acquired in her first copulation, there is one limited locality where the female is especially vulnerable to a reproductively motivated male, i.e. her burrow. If the nest entrance is left open during the time the female is provisioning a cell, males easily can identify the spot where a female is likely to be and hence where mating is likley to occur. Moreover, the burrow opening is a small area well suited for defence. Note that a strategy of nest territoriality is linked with a relatively long life for the males of a species.

At the other end of the spectrum, if fertilizable females are likely to appear unpredictably over a broad area, then territorial behaviour is probably a waste of time and energy. Under these circumstances, non-aggressive, wide-ranging sorties in search of females may be the optimal strategy. In the Nyssoninae, females apparently are fertilized usually just once, shortly after emergence. Moreover, nests containing virgin females often are scattered widely in homogeneous sand dunes or barren wastes. Sand wasp males typically perform a 'sun dance' in which the male courses widely back and forth a few inches over the ground pouncing on all things remotely resembling a female (Evans 1966b).

If, however, there are cues that indicate a certain part of the nesting habitat is superior to others (e.g. the non-random distribution of male emergence holes for *S. speciosus*), then males that aggressively secure prime areas for themselves may enjoy a reproductive advantage. For example, if there are a limited number of perches which give a male a special vantage point to scan for females or which are in some way actually attractive to females, then an investment in their defence may result in extra opportunities to copulate.

Although these arguments are somewhat speculative, they may suggest useful ways of interpreting male behaviour in wasps. Tests of the validity of these ideas can be provided by additional comparative data. Bohart & Marsh (1960) provide a possible example of a species in which males either defend a small area or engage in non-aggressive patrolling. An identification of the conditions promoting both territorial and non-territorial reproductive strategies within this or other species would be especially instructive.

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