

MALE TERRITORIAL BEHAVIOR IN FOUR SPECIES OF THE TRIBE CER CERINI (SPHECIDAE: PHILANTHINAE)

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Abstract.—Males of four species of Cer cerini have been found to defend territories and to scent-mark stems on the peripheries of the territories: *Eucerceris flavocincta*, *E. cressoni*, *E. superba*, and *Cerceris nigrescens*. Males of *E. flavocincta* form aggregations resembling leks in which large males are more likely to maintain possession of a territory because of their advantage in aggressive interactions. Data are also presented on nest distribution and prey of these species.

Males of most species of Philanthinae possess hair brushes on the clypeus associated with the aperture of their large mandibular glands; the same species also possess varied patterns of hairs on the venter of the abdomen. Males of many of these species are known to be territorial and, via a behavior referred to as "abdomen dragging" (Alcock, 1975a), probably scent-mark grass stems on the margins of their territories. Recently, it has been confirmed that volatile chemicals originating in the mandibular glands are applied to stems by territorial males of *Philanthus* (Schmidt et al., 1985). It is thought that the pheromones are applied to the stems with the clypeal hair brushes and subsequently spread with the abdominal hairs as they come into contact with the marked portion of the stem as the male walks forward (Gwynne, 1978). Evidence suggests that the pheromone is attractive to females, as most matings that have been observed occur within territories (e.g., Gwynne, 1980; O'Neill, 1983b).

In the tribe Cer cerini, the clypeal hair brushes are shorter and directed downward, as compared to *Philanthus*, where they are directed toward the midline. Also, the abdominal hairs tend to be poorly developed or, as in many *Eucerceris*, confined to bands on one or more sternites. Territoriality and scent-marking have been less frequently reported in the Cer cerini than in *Philanthus*. Steiner (1978) described an aggregation of male *Eucerceris flavocincta* in Oregon in which individuals were territorial for short periods, and Alcock (1975b) reported briefly on territoriality and scent-marking in *E. arenaria* Scullen, *E. canaliculata* (Say), *E. rubripes* Cresson, and *E. tricolor* Cockerell from localities in Arizona and New Mexico.

In this paper we report on four species of Cer cerini observed in Colorado: *Eucerceris flavocincta*, *E. cressoni*, *E. superba*, and *Cerceris nigrescens*.

RESULTS

Eucerceris flavocincta Cresson

An aggregation of males was discovered in mid-July 1979 in an intermountain valley known as Stove Prairie, 45 km west of Fort Collins, Colorado, at an altitude of 2,200 m. Males occupied a rocky outcrop adjacent to a grove of ponderosa pines and juniper. Males were abundant on this same outcrop in July 1981 and again in

July 1982, when most of our studies were made. The number of territories on the outcrop varied from four to about 20 on various days, with a total of 30 different territories identified in 1982. In addition, there were a few isolated territories in a meadow 100 m or more from the outcrop. These occurred in bare spots surrounded by grasses and weeds and were mostly widely spaced, at least several meters apart. In contrast, territory density at the outcrop was much higher. For example, 17 territories occupied on 22 July 1982 were only 1.5 m apart on average ($SD = 0.7$; range = 1.0 to 4.0).

Behavior of males on territories consisted primarily of orienting to and pursuing passing insects and aggressive interactions with conspecific males. Males perched on rocks or low branches of trees or bushes, assuming an "alert" posture, with the head tilted slightly upward, the antennae held rigidly forward or upward, and the wings held obliquely upward (as illustrated by Steiner, 1978). Males frequently moved the head slightly or rotated their entire body to face in a different direction. Flights from perches were frequent (mean = 6.4/min; $N = 76$ for 5 individuals) and of two kinds: slow circling flights over a radius of about a meter from the perch, often appearing "exploratory," but sometimes leading to scent-marking; and very swift, straight flights, sometimes two or more meters in length and sometimes in obvious pursuit of another insect. While pursuing insects of other species, particularly syrphid flies, which were common here, the territory resident followed behind and below, without making contact. However, interactions with conspecific males were quite different in form. When a conspecific male flew close by, the result was pursuit and often a tight "swirling flight" (Alcock, 1975a), but also commonly escalating into intense bouts of butting and grappling. These interactions were common and as intense as those observed in some species of *Philanthus* (e.g., Gwynne, 1978; O'Neill, 1983a) and occurred between a territory resident and either an intruder or a male on an adjacent territory. As many as six males were observed simultaneously interacting within a single territory. The head butting interactions, which usually occurred in mid-air, produced a clicking sound audible several meters away. If a conspecific male landed on the ground near a territorial perch, the two often approached head on (sometimes circled one another in the process) and grappled with their mandibles and forelegs, with considerable buzzing. Wrestling males sometimes fell from the perch to the ground (up to 3 meters below) while remaining locked together in combat. These interactions commonly ended with the original resident of the territory leaving and the intruder usurping possession of the perch. In 20 interactions in which we could identify which male was the resident, the intruder usurped possession of the territory seven times (35%). Steiner (1978) reported behaviors similar to those above in the Oregon population.

As in *Philanthus* (O'Neill, 1983a, b) the outcome of aggressive interactions by males in this population was dependent on the relative body sizes of opponents, rather than their status as resident or intruder. In 1982 we captured 120 males, measured their head widths to the nearest 0.1 mm with a pair of VWR Scientific Products dial calipers, gave each individually distinctive markings with dots of colored enamel paint, and released them. This allowed us to monitor the outcome of aggressive interactions with respect to the body sizes of contestants. In twenty interactions in which we knew the body size of both contestants, the winner was larger 14 times, in the same size class 6 times, and never smaller.

Because of the size advantage enjoyed by larger males and the large numbers of males present relative to the number of the territories many males not defending territories were present at any given time. These males had at least two options for obtaining territories. First, they could aggressively usurp a perch from a resident male. Second, they could enter and occupy a territory abandoned by a resident for some reason. This abandonment and replacement was commonly observed and we could artificially induce it by removing a resident from a territory and allowing other males to occupy it. The methods for accomplishing this have been described previously (O'Neill, 1983b). By repeating the removals, we could cause as many as 14 males to occupy a single territory in one day (mean = 3.8 residents; SD = 4.0; range = 1 to 14; N = 10). Of the 48 males removed from territories during these experiments 37 were replaced within 30 minutes by another male; three other times males were replaced, but after intervals of 33 to 72 minutes. The mean time between removal and replacement was only 9.4 minutes (SD = 14.3; range = 1 to 72; N = 40). When the first male ("original resident") removed was replaced, he was usually replaced by a smaller male (seven of eight times; chi-square = 4.5, $P < 0.05$). However, when subsequent residents on the same day were removed, they were replaced by smaller males on 42% of the time (N = 28, chi-square = 0.57, not significant). These results are similar to those obtained on three species of *Philanthus* (O'Neill, 1983a, b).

As also noted by Steiner, males usually persisted at a perch for a short period, often only a few minutes. There were exceptions however. A male marked white-green (the largest marked male in the population) occupied a territory on the morning of 19 July from 1017 until 1129. In one 20 minute interval during which he was observed continuously, he successfully defended his territory 21 times. Another male, marked blue, was present on a territory on 6 July from about 1000 to 1116. However, males were never observed to defend a territory on any given day for the long intervals (i.e., several hours) commonly observed in territorial male *Philanthus* (e.g., O'Neill, 1983a).

Males were seen scent-marking on twigs, sagebrush, grass stems, pine needles, and other plants near their perches, but, without exception, this behavior was extremely brief, rapid, and always in one direction (up) on the stem. While the body was pressed close to the stem, there was no V-shaped posture as described for some species of *Philanthus* (e.g., Alcock, 1975a). Some males (e.g., white-green discussed above) were not observed to scent mark at all, while others did so relatively frequently. One male (blue) scent-marked 4 times in 66 minutes of observation; another (unmarked) scent-marked 16 times in a 20 minute interval. It is noteworthy that *E. flavocincta* is the only species of its genus lacking the transverse bands of close-set hairs on the ventral side of the abdomen (Scullen, 1968). There are, however, abdominal hairs which are fairly dense on the last four sternites.

Two instances of attempted mating were observed in places where territories were aggregated. Steiner (1978) reported observing a copulating pair, presumably in the aggregation of males he was studying. We also captured two females and released them near territorial males. In both cases a swift pursuit resulted.

We spent many hours in an effort to locate nests of females, but after covering much ground, found only one small plot of bare soil 50 m from the territorial area, where three females started nesting on 22 July. One nest was excavated on 2 August; there were five cells at depths of 7 to 11 cm, each provisioned with 3 to 6 weevils,

all of one species, *Orimodema protracta* Horn (Curculionidae). Thus, we obtained the impression that the nests must be widely scattered in this area. Observations in other locations agree with this judgement. An isolated nest found on 7 July 1982 on a path in Hewlett Gulch, several km from Stove Prairie, was also being provisioned with *O. protracta*. Still another, apparently isolated nest was found in Yellowstone National Park, Wyoming, on 12 August 1971; it was being provisioned with the weevil *Trichalophus alternatus* Say. Evans (1970) also reported an isolated nest from Jackson Hole, Wyoming. On the other hand, Scullen (1939) noted "several dozen burrows" extending over "an area as large as the average city block" in Oregon. Also, Bohart and Powell (1956) reported "thousands of burrows" in silt and gravel hills in Sierra County, California. Thus it appears that females do nest in aggregations in some places, but male behavior has not been reported from such sites.

Steiner (1978) noted that there appeared to be no resources for females (i.e., flowers that might serve as nectar sources) within the aggregation of males. This was also true at Stove Prairie, and furthermore, the soil within the territory aggregation was rocky and overgrown with grasses and sage, thus evidently not suitable for nesting.

Eucerceris cressoni (Schletterer)

As in the preceding species, *E. cressoni* is characteristic of montane regions of the western United States. It is a smaller species and, unlike *E. flavocincta*, it possesses a dense, transverse band of fimbriate hairs on the fifth sternite of the males. This species has commonly been called *fulvipes* Cresson and is so called in the recent *Catalog of Hymenoptera in America North of Mexico* (Krombein et al., 1979). Bohart and Menke (1976) regard *fulvipes* as preoccupied.

Our studies were conducted 22 km west of Livermore, Larimer Co., Colorado, at an altitude of 2,350 m. The species is abundant in late summer, especially on flowers of *Solidago* spp. We found individual males to have established territories at two sites along the sides of a canyon and at one site in a meadow at the floor of the canyon, 11–12 August 1984. These three sites were 200–300 m apart, but there may have been other territories in between that we did not find.

In the sites on the hillside, the males perched on dead, prostrate branches of bushes, surrounded by grasses and sagebrush. In the meadow below, a male had established a perch on a dried cattle dropping surrounded by grass. All three males defended their territories vigorously and scent-marked surrounding vegetation at rapid rate. While perched, they held their antennae rigidly forward and their wings obliquely upward, as described for *E. flavocincta*.

Our more detailed observations were made at the territory closest to the top of the canyon. During a 10-minute period (1036–1046), the resident male scent-marked nearby grass blades 54 times in 41 bouts, sometimes marking 2–5 stems per bout. Between each bout he returned to his perch on dead branches of a bush, less commonly on grass blades. During this period, he interacted four times with a conspecific male, following closely behind in flight and occasionally butting the intruder. During a second 10-minute period (1107–1117) on the following day, the male resident on this territory scent-marked 36 times in 20 bouts and had two interactions with conspecific males. At 1248 on this same day, the resident male was still defending

the territory and scent-marking (21 times), but he left the territory at 1253 for the day.

In all but one of the scent-markings observed, the wasp walked only upward along the stem, not reversing itself as commonly occurs in *Philanthus*. In every case the head and posterior part of the abdomen were pressed against the stem, in a broadly V-shaped posture. From 3–5 cm of the plant were covered in each episode of abdomen dragging.

We made an extensive search for nests in the vicinity of these three territorial sites, but were only able to find one, on 26 August, along a road cut at the top of the canyon, about 150 m from the uppermost territorial site. The nest entrance was beneath a loose rock, in sandy loam. Prey had been stored in the burrow, at depths of 9 and 12 cm, and there were two cells, at depths of 12 and 14 cm, containing 5–7 prey each, with an egg laid longitudinally on top of the prey. All 15 prey were of similar size and form, but consisted of three species, *Otiorhynchus ovatus* (L.) (11), *Anametis* spp. (3), and *Listronotus obscurellus* (Dietz).

Evans (1970) reported finding a group of nests in the midst of an aggregation of *Philanthus crabroniformis* in Jackson Hole, Wyoming, the prey consisting of three species of weevils. Evidently, this species does group its nests in suitable areas of bare soil at times.

Eucerceris superba Cresson

This large species is characteristic of the Rocky Mountains and western Great Plains, usually in less wooded areas than the preceding two. Males of this species have three transverse bands of fimbriate hairs, on the third, fourth, and fifth abdominal sternites. Both sexes are common visitors to *Eriogonum effusum*. We made brief observations on male behavior at the Great Sand Dunes National Monument, Alamosa Co., Colorado, at an altitude of 2,450 m, 10 August 1983. Two males were seen grappling at 1012 in an area of sparse grasses, cacti, and yuccas on the crest of a small sand hill adjacent to the dunes. The smaller of the two males left the area and the larger maintained a territory in a partially bare area about 1.5 m in diameter. This male perched mainly on the ground, but also on low plants. All scent-markings were on grass blades, and all were upward only, the wasp sometimes covering up to 15 cm on a single marking, assuming a broadly V-shaped posture, with the head and posterior part of the abdomen pressed close to the grass blade.

Over a 10-minute period (1015–1025), this individual scent-marked 27 times in 15 bouts, bouts containing markings on up to four separate grass blades. During this time the male also pursued passing insects.

Scullen (1939) quoted field notes by O. A. Stevens to the effect that males patrol for females and attempt to mate with them on flowers. Stevens also reported a female carrying a weevil, *Ophryastes sulcirostris* Say, in North Dakota. Scullen (1968) later gave a record of a weevil of the same genus taken as prey in Alberta. Evidently nests of this species have never been found.

Cerceris nigrescens F. Smith

This species is widespread in North America, occurring from coast to coast. The males have fimbriae of short, clumped hairs emanating from sternum VII and ap-

pressed to sternum VIII. Brief observations on this species were made on 28 June 1984, in Hewlett Gulch, 35 km northeast of Fort Collins, Colorado. However, since scent-marking has not previously been reported in this genus, we thought it of value to include the observations in this paper. At 1050 a single territorial male was found on a rabbitbrush (*Chrysothamnus*). The male alternated perching on the plant (15–30 cm off the ground) with flights around the plant, sometimes in pursuit of passing insects. When perched the male adopted the posture described above for *Eucerceris*. The male scent-marked plants, usually the rabbitbrush, walking either up or down the stem, but not assuming a V-shaped posture. During a 15-minute observation period, the male scent-marked 15 times, in bouts of one to three abdomen drags. A search of the area near this territory revealed no other males.

C. nigrescens is reported to nest in sandy soil, either as solitary individuals (Peckham and Peckham, 1898), in small aggregations (Evans, 1971), or in groups of as many as 50 females within 10 square feet (Krombein, 1936).

DISCUSSION

Population size and nest density of many Cercerini appear to vary greatly. As noted, species of *Eucerceris* and *Cerceris* have been found to have either solitary, scattered nests or to nest in large aggregations. Byers (1978) described great yearly variation in populations of *C. halone* Banks in Virginia. At one site, there were 407 nests in 1967, but only 26 in 1975, and none in 1977. Alcock (1975c) was able to greatly increase the density of nests of *C. intricata graphica* F. Smith (identified as *simplex*) by watering the soil. The unpredictability of nest site occupation by Cercerini stands in contrast to that in *Philanthus*, where populations of several species are known to have been more or less constant at certain sites over many years (e.g., Evans, 1973; O'Neill and Evans, 1983). Since nest distribution is an important factor influencing male mating tactics (Alcock et al., 1978), one might anticipate greater lability in mating systems in Cercerini than in *Philanthus*. Unfortunately, data bearing on this point are fragmentary.

There are many similarities in male territorial behavior of some Cercerini and of *Philanthus*. Males of several species defend territories vigorously with basically similar interactions and scent-mark stems on their territories. It appears that in *Eucerceris* scent-marking males pass only upward along the stem, rather than up and down as in species of *Philanthus* and in *Cerceris nigrescens*. The consistency and significance of this behavioral difference remain to be determined. As in *Philanthus*, there is intense competition for territorial sites and larger males are most successful in maintaining territories. Removal of resident males of *E. flavocincta* usually resulted in occupation of the territory by one of the many non-territorial males present in the area in less than 10 minutes. As in *Philanthus*, rates of scent-marking are lower in the larger species. Many species of *Cerceris* do not appear to exhibit male territoriality or scent-marking. Alcock (1975b) noted that this is the case in *C. frontata* Say and *C. intricata graphica* (identified as *simplex*), two species in which males patrol broad areas for receptive females.

The mating system of *E. flavocincta* appears similar in many respects to that of *Philanthus basilaris* (O'Neill, 1983a). In both species, scent-marking territorial males gather in dense groups to attract receptive females. These "leks" may have evolved

because of the unpredictability of the widely spaced and difficult to locate nests of females, at least in the populations studied by Steiner and us. It will be interesting to see if this mating system prevails in large aggregations such as those studied by Scullen (1939) and Bohart and Powell (1956).

The subfamily Philanthinae appears to be at least as old as 25 million years, since fossils identified as *Philanthus* and *Cerceris* have been discovered in Oligocene deposits. Male territoriality and scent-marking have now been reported in four genera of Philanthinae: *Philanthus*, *Eucerceris*, *Cerceris*, and *Clypeadon* (Alcock, 1975b), including representatives of all three main divisions of the subfamily recognized by Bohart and Menke (1976). Thus, "abdomen dragging" and the associated morphological adaptations (i.e., clypeal and abdominal hair brushes) are probably relatively ancient characters within this group. It seems less plausible that these adaptations have evolved independently as the subfamily has radiated. However, it is evident that there is much evolutionary plasticity in these characters, given the variability in their expression among species. They are most developed in *Philanthus* where most species have highly developed clypeal and abdominal hair brushes and may have extremely high rates of scent-marking. In contrast, some species do not exhibit territoriality and lack well-formed clypeal or abdominal hair brushes. Alcock (1975b) noted that this is the case in *Cerceris frontata* and *C. intricata graphica* (identified as *simplex*). Reduced mandibular glands and the loss of clypeal and abdominal hair brushes in *P. albopilosus* is most likely associated with the fact that, rather than defend territories, males of this species patrol for females in open dune areas (Evans, 1975). It appears that some form of territoriality and scent-marking is ancestral in this group, the behaviors have diversified and, in some cases, secondarily disappeared in the face of the varying selection pressures that mold mating systems.

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