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## The behaviour of western cicada killer males, *Sphecius grandis* (Sphecidae, Hymenoptera)

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### Introduction

This paper compares the behaviour of male western cicada killers, *Sphecius grandis* (Say), with the eastern cicada killer, *S. speciosus* (Drury), subject of Norman Lin's classic paper (1963) on male territoriality in wasps.

The study was conducted between 10.xiii.74 and 17.xiii.74 at a site approximately 2 km W of the Southwestern Research Station near Portal, Arizona in the Chiricahua Mountains, at an elevation of 1980 m. A group of 100-150 males resided in a female nesting area roughly 7 m × 15 m bordered by a dry stream bed. Nest entrances, emergence holes and perch locations were scattered along a vertical 2 m high bank on one side of the wash as well as on the sloping opposing bank (a grassy incline). Two large piles of branches and other debris dominated the nesting area which was surrounded by a grassy clearing set in an oak-pinyon woodland. At the time of the study few females were present and I saw only one instance of nest provisioning. I conducted 1-5 daily censuses of marked males; a total of 19 received a distinctive dot or dots of acrylic paint on their thorax.

### Perches and perch attachment

Males perched on a wide variety of substrates: stumps, fallen limbs, blocks of wood, weed heads, flowers and stems, pebbles, bare patches of soil by emergence holes, grass blades and tree branches from less than 1 m to about 7 m above the ground. Males could be found on their perches, in the typical sphecid alert posture with front legs drawn up (fig. 1), from 0736 Mountain Standard Time to at least 1730. The peak of male activity occurred in the early morning from 0830-1000. A few males emerged from their sleeping places (emergence holes) as early as 0642-0700 at a time when the area was completely shaded. These early risers flew to trees, presumably to feed on sap as reported from *S. speciosus* (Lin, 1963).

By following the contingent of marked males, I established that most individuals exhibited a strong attachment to a specific perch returning to it repeatedly after launching sallies in pursuit of passing insects (table). Three of ten males marked on 10 August held the same perch for the entire study (8 days); the overwhelming majority of those marked returned to a particular perch for two or more days running. There was, however, individual variation in the degree of perch attachment. Two males alternated continually between two sites (less than 1 m and about 2 m apart respectively). Four marked males were known to change perches (in 51 wasp-days of observation) adopting

a total of seven new posts. The average distance between old and new perches was about 4 m (range, 0.5–12 m). In addition, I frequently saw unmarked males on the perches of marked individuals during times when the regular owners were temporarily absent. This suggests that some males float through the population looking for a new perch (or their first regular one).

The number of days that marked male wasps remained on a specific perch

	Days on perch							
	1	2	3	4	5	6	7	8
10 males marked 10 Aug.*	2	1	3	—	1	—	—	3
1 male marked 12 Aug.	—	—	—	—	—	1	—	—
8 males marked 14 Aug.	2	2	—	4	—	—	—	—

\* Study ended 17 August.

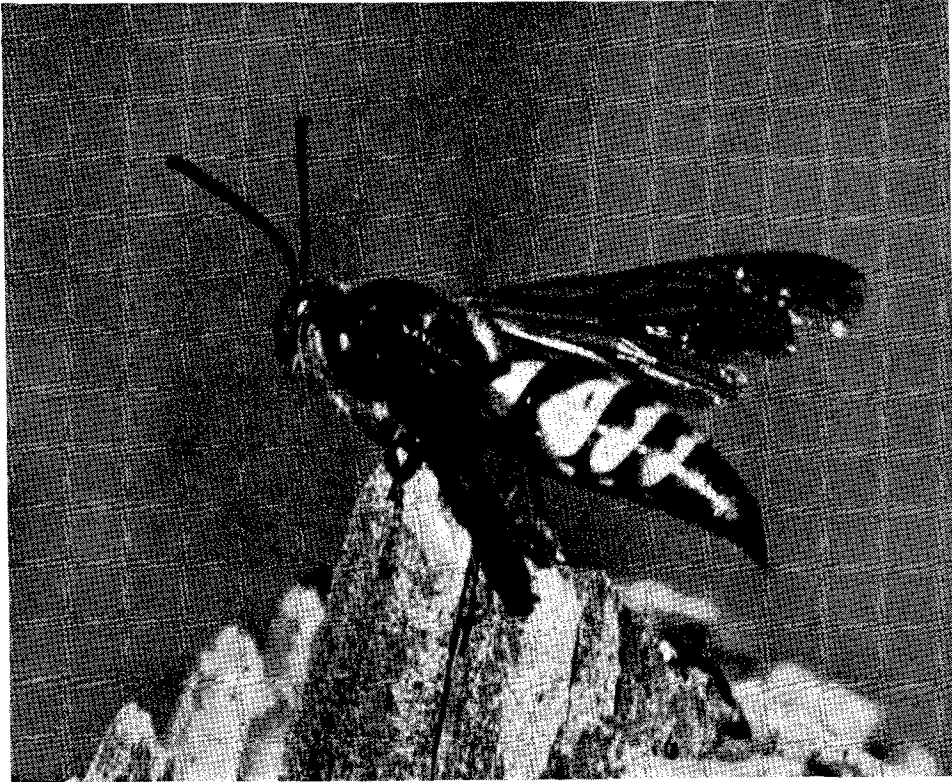
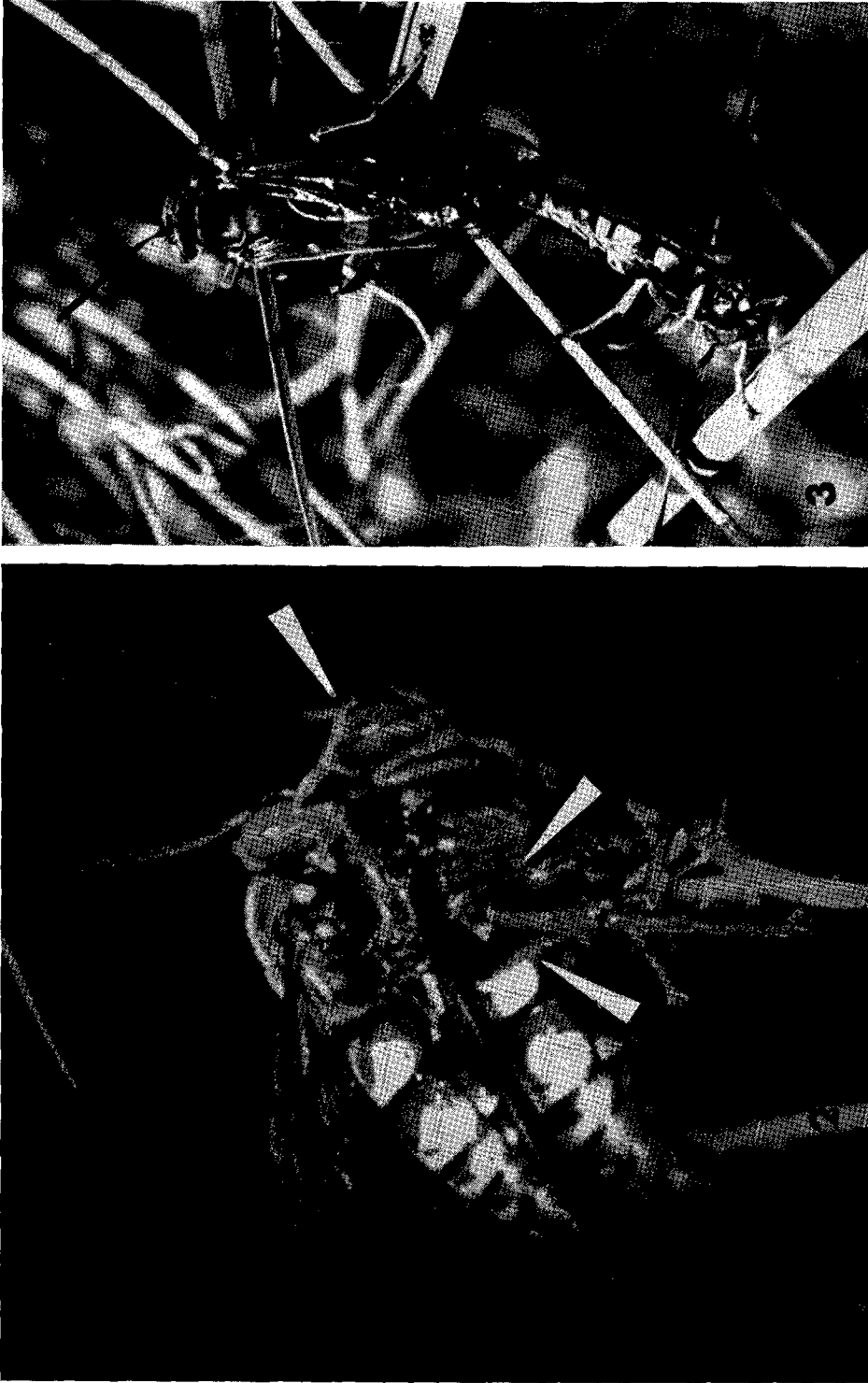


FIG. 1. A male *Sphecius grandis* in its alert posture on its perch, a weathered tree stump. Photograph by George Gamboa.

### Territorial behaviour

Despite a high population density (occasionally as many as 10 males could be found swirling through the air over a single square metre) each male generally had a well defined perch site occupied only by itself. Often the perches were separated by a metre or less (as little as 50 cm). The site tenacity exhibited by the marked males would seem to indicate that the species is



FIGS. 2-3. (2) A pair of cicada killers in the pre-copulatory pose. The arrows point to the position of the legs of the male; note the location of the forelegs. (3) A mated pair of *S. grandis* with the female above the male. Photograph by George Gamboa.

territorial. Moreover, perched males did pursue other males, sometimes capturing them in flight and grappling in mid-air, often with one male holding the other by its head or thorax for several seconds. Nevertheless, it is at least possible that this does not constitute aggressive defence of a territory. Instead the pursuing male may simply treat all passing insects as potential females, which must be captured in flight prior to mating. The regular spacing of males might be the outcome of individuals seeking unoccupied vantage points rather than the active exclusion of one male by another defending its territorial space. Lin (1963) feels strongly however that males behave differently toward an intruder of their own sex as opposed to a passing receptive female. He interprets the approach of one male to another as threat behaviour, an interpretation that I do not believe applies to *S. grandis*.

### Mating behaviour

Two matings, initiated at 1208 and 1340, and several unsuccessful attempts at copulation were seen. Males pursued and grasped females in flight, whereupon the couple either flew directly to a tree or tumbled to the ground alighting on vegetation or debris. Initially the male rested on the back of the female (fig. 2) with his midlegs grasping the female's thorax just behind her wings forcing them slightly out and presumably making escape flight more difficult. The male's hindlegs encircled the female's abdomen while the tarsal claws of the forelegs tapped lightly and rapidly on the dorsum of the female's eyes by the base of her antennae. The male's antennae were held upward and did not lash the female's antennae in the one case where I had an opportunity to observe this carefully (antennation by the male has been reported for *S. speciosus* by Reinhard, 1929). Receptive females permitted coupling to occur when the male twisted his abdomen down and under the female touching his genitalia to the genital opening of his mate. After insertion of the aedeagus the male quickly dismounted and turned 180°; females on the ground took flight at this point with the male trailing behind. The mated pair flew to branch tips about 6 m above the ground where the female grasped foliage while the male dangled behind her (fig. 3). In one case a pair remained in copulo for at least 80 min.

### Discussion

The behaviour of *S. grandis* is similar to that of *S. speciosus* in many respects (Lin, 1963, 1966, 1967):

- (1) 'Territorial' males hold perches in a female nesting area.
- (2) Males occupy perches from roughly 0800–1800, with a morning peak of activity.
- (3) Males often return to one perch over several days.
- (4) Males pursue passing insects and grapple with other males in flight.
- (5) Mating is initiated when a flying male grasps a flying female; copulation begins with the male on the dorsum of his mate; the male subsequently dismounts to complete a prolonged copulation in an end-to-end position.

Differences between the species appear to involve relatively minor details. In the population Lin studied, the overwhelming majority of males (52 of 56

in one sample) held perches by an emergence hole on the ground whereas the majority of males I watched had adopted an elevated perch. This probably corresponds to a difference in nesting areas, Lin's study site being a barren and much used pathway in a Brooklyn park. In the absence of elevated perches his wasps may have settled for the only conspicuous perch marker—an emergence hole. In this regard, it is significant that on the Harvard campus, *S. speciosus* males perch on dormitory steps and low bushes rather than on the ground (Howard Evans, personal communication).

Lin found that territory size in *S. speciosus* was a minimum of 1.3 m × 1.3 m whereas in the Chiricahua area the personal space about a perched male was often about one-half this figure. Lin (pers. comm. in Evans, 1966) states that the system of perch ownership breaks down in extremely dense populations of the eastern cicada killer. Despite a high density of *S. grandis* in the study area the spacing system of the males retained its integrity.

### The mating strategy of *S. grandis*

*Sphecius* males must compete for a limited population of virgin females because mated females reject courting males (Lin, 1963). Females nest gregariously and provision many cells in one nest. Because males emerge before females, the presence of emergence holes provides a good indicator of where virgin females are likely to come out. Therefore, a male that secures a perch site in an area with many emergence holes may have superior opportunities to detect and capture a fertilizable female (Lin, 1963). In any event, some perches are surely better than others, which favours males that retain possession of a good vantage point from which to spot and pursue passing females. This leads to the perch attachment shown by most males but may also produce the perch changers observed in this study, as some males abandon peripheral or otherwise unsuitable locations in favour of potentially more productive ones. Regular flights out from a perch permit the resident male to inspect his surroundings carefully. The pursuit of other males may (1) identify them as inappropriate mates, (2) aggressively drive them away from a superior location, or (3) simply alert the pursued insect that the area is already occupied, leading the 'intruder' to go elsewhere.

Males of other species of sphecids are known to occupy and defend perches in or near a nesting area (see review by Alcock, in the press). Because very few studies have involved marked individuals, it is usually not known whether a male may retain a perch over a period of days (as in *Sphecius*, *Philanthus triangulum*—Simon Thomas & Poorter, 1972) or whether occupation of a perch is purely temporary (as in *P. multimaculatus*—Alcock, in the press, *Eucerceris arenaria*—personal observations). Given the limited amount of comparative data it is difficult to solve the problem of why males of some species should exhibit a prolonged attachment to a given perch while others abandon a site after holding it for a few hours. Nevertheless, in my experience, males of those species that take up temporary residence at a perch always use the location for calling purposes, laying down an attractant pheromone by dragging the underside of their abdomen over nearby twigs and stems while watching for approaching females from the perch itself. For these males the value of a perch lies not so much in its location as in what has been added to the perch.

Because a male can mark any one of a number of perches and thereby make them attractive, it may not pay to reclaim an old perch, especially if it is already occupied by another individual. Instead the male may simply select a new spot and apply his calling pheromone there.

There is no indication that *Sphecius* or *P. triangulum* employ an attractant pheromone. For these species the *primary* value of the perch presumably resides in its location (in an area where relatively many fertilizable females may appear) and in its utility as a vantage point for scanning the environment for virgin females. Unlike a perch that requires a pheromone to become useful, the scanning perch retains its value from day to day and therefore it may pay a male to return to it time and again.

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