

## Male Territoriality and Nesting Behavior of *Calliopsis hondurasicus* Cockerell (Hymenoptera: Andrenidae)

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**ABSTRACT:** *Calliopsis (Calliopsis) hondurasicus* is the most widely distributed member of its genus, found from the southern United States throughout Mesoamerica, yet little has been recorded about its biology. Female nesting behavior and male territorial behavior are described for a population on the Pacific coast of central Panamá. This population is protandrous, and bees become active at the start of the dry season in mid- to late-December, and activity ends in late January or early February. Males patrol areas where females emerge and later nest, and they defend territories to which they return repeatedly. Male-male contests involve a rapid spiraling-upward flight, often followed by physical aggression after the pair tumbles to the ground. Nearly all females are solitary nesters, but they dig nests within aggregations near other females. Details of nest architecture are given for comparative purposes. At this site females are restricted in their use of pollen, which may constrain the number of generations they produce per season.

Bees in the subfamily Panurginae (Andrenidae) are abundant in the deserts of North and South America, but are not well represented in the neotropics (Rozen, 1967, 1989; Michener, 1979; Ruz, 1991). The genus *Calliopsis* (Hymenoptera: Andrenidae) includes approximately 78 species in 11 subgenera, mainly from North America + México and South America (Ruz, 1991). As with other panurgines, many *Calliopsis* species appear to be pollen specialists (oligolectic) (e.g., Rozen, 1967; Shinn, 1967; Visscher and Danforth, 1993; see Wcislo and Cane, 1996). *C. (Calliopsis) hondurasicus* Ckll. is the most widely distributed *Calliopsis*, extending from Louisiana, U.S.A., southward through Mesoamerica to Panamá, and is the only *Calliopsis* found in Central America (Michener, 1954; Shinn, 1967). Despite its extensive range, little has been published on its biology, other than anecdotal observations on nest architecture (Prof. Alvaro Wille, cited in Shinn, 1967); nothing is published on male behavior. This report describes aspects of the nesting and mating behavior of *C. hondurasicus* as a contribution to comparative studies of panurgine bees (cf. Rozen, 1967, 1989), and to provide a basis for forthcoming experimental studies (Wcislo, in prep.).

### Materials and Methods

**STUDY SITE:** This report is primarily concerned with a population found at the "Parachute Drop Site" at Fort Kobbe (8°53'28"N, 79°36'14"W), a U.S. military base adjacent to Playa Kobbe, near Veracruz, Panamá Province, Republic of Panamá. The site is a large open field that is regularly mowed, surrounded on three sides by deciduous tropical forest, and by the Pacific Ocean on the fourth side. I made preliminary observations during January, 1996, but most observations were made i) between 10 December 1996-10 February 1997, and ii) 3 December 1997-17 January 1998. At times U.S. military officials prohibited observations at the site.

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Juan Carlos Perez esp. de sp. collected  
March 8 April  
Calliopsis Panay San Lorenzo, P.O. San Juan

**MALE BEHAVIOR:** Males were marked by placing unique combinations of Testor's enamel paint on the dorsal surface of the thorax, and body size (intertegular distance) was measured using Mitutoyo digital calipers. Within the nest aggregation, one section ( $\sim 10 \times 20$  m) was divided into 50 cm<sup>2</sup> quadrats with a string grid (December 1997), and the density of emergence holes and nests per quadrat was measured. Territory size was estimated by counting the number of quadrats included in the area each male patrolled; a quadrat was counted if the male used at least  $\sim 50\%$  of the area. Territory size was based on 1 day of observation for each male, and 2 or 3 males were observed concurrently each day for  $\sim 3$  hours of observation during peak activity ( $\sim 9:00$ – $12:00$  hr). Within each quadrat, the number of nests and emergence holes was counted on the same day that behavioral observations were recorded. These holes were examined with a micro-bore viewing scope (Titan Tool Supply, Buffalo, NY) to inspect a hole/nest to a depth of 25 cm; nests could be distinguished reliably from an emergence hole only if a resident bee was observed, so in most cases emergence holes and nests were not distinguished.

**FEMALE BEHAVIOR:** Individual nests were marked with nails placed in the soil, and females were marked as described above for males. Foraging behavior of females was observed by monitoring their activity at nest entrances, several nests at a time. Transparent plastic cups with screens were placed over the nest entrances to briefly hinder a bee's entrance or exit. As the bees took flight while exiting, or approached the nest while entering, the cups were removed, and the bee's identity noted.

**NEST EXCAVATIONS:** Nests were excavated using standard techniques. A thin slurry of plaster-of-Paris and water was injected into the nest tunnel using a plastic syringe. Nest cells were then excavated by slowly removing the soil with a pocket knife, following the tunnel into the soil via the hardened plaster cast. Cells were opened and the contents transferred to a well of a plastic tissue culture tray; the interior of the cells was examined later under a dissecting microscope. Pollen was identified using keys in Roubik and Moreno (1991).

Throughout the paper, means are given with standard deviations. Statistical analyses were made on a personal computer using SYSTAT v7.0.

Voucher specimens are in the dry reference collection of the Smithsonian Tropical Research Institute, and in the Museo de Invertebrados "Graham Fairchild," Universidad de Panamá.

## Results

**SUMMARY OF SEASONAL ACTIVITY AND LIFE-HISTORY:** The Pacific coast of central Panamá receives about 1500 mm rain per year, and has a pronounced dry season with little or no rain from approximately mid-December through April. Many trees are deciduous, and grasslands become so dry they readily burn. *C. hondurasicus* is abundant and commonly encountered nesting in open, exposed areas in this region during the beginning of the dry season. Flight activity can begin as early as mid-November and continues through early February (Michener, 1954; pers. obs.). I have not collected this species on the Caribbean slope nor along the Atlantic coast of Panamá, where annual rainfall is higher ( $>3000$  mm) and there is not a strong dry season; there are no published records of this species from the Caribbean side (Michener, 1954).

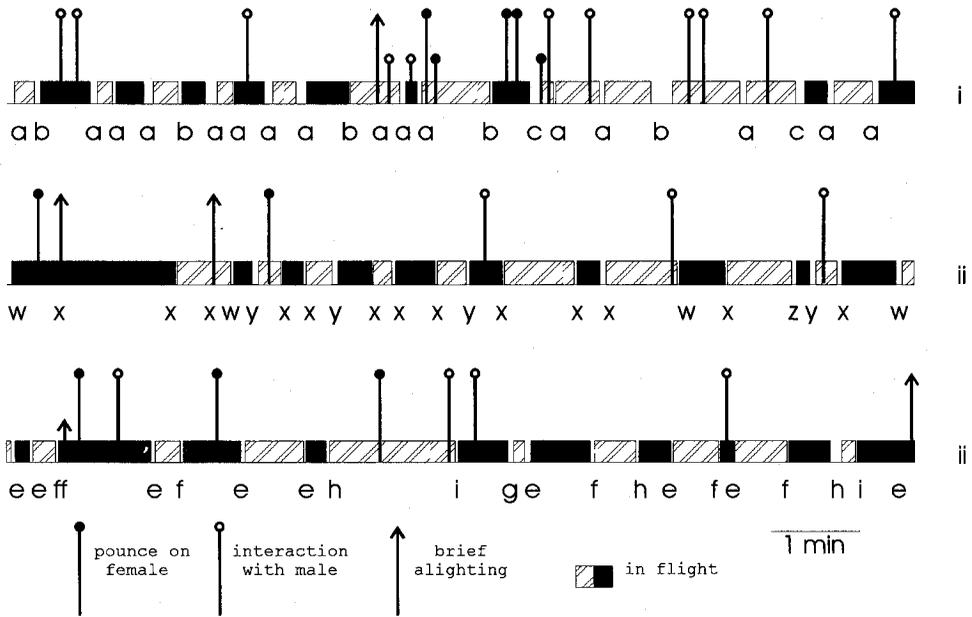


Fig. 1. Schematic diagram of territorial behavior of 3 male *Calliopsis hondurasicus*; each line (i–iii) represents a different male. The shaded area indicates that males are flying, broken by white areas when the male has perched; different shadings are used for clarity only. Letters under the white areas indicate different perch sites. Symbols indicate interactions with conspecifics, or momentary (<1 sec) alighting on perch; different heights are used for clarity only.

Males and females diapause as prepupae within underground cells, and emerge as active adults in mid-December. The population is protandrous: in 1995, males were first observed on 17 December, and females were already flying on 7 January 1996, which was the next visit; males were first observed on 6 and 13 December 1996–1997, respectively, while the first females were observed flying on 11 and 17 December 1996–1997, respectively.

Males fly over the site and attempt to mate with emerging females, and with females just starting to excavate nests. After a female has begun excavating a nest, she usually rejects males that attempt to mate with her ( $N > 100$  attempted matings). Females repeatedly forage for pollen and nectar that they use to provision cells during late December and January. Throughout January mating activity gradually diminishes and males gradually disappeared from the site; presumably they died. The latest dates a male was observed flying was 25 January, 7 February, and 6 January, 1996–1998, respectively.

**MALE TERRITORIALITY:** Males spend the night in shallow burrows that they excavate near the area where females are nesting, as reported for *C. (C.) andreniformis* (Shinn, 1967). They patrol the nesting site, although some also were flying around nearby legume flowers. The mean size of males patrolling at the nesting site was  $1.25 \text{ mm} \pm 0.035$  ( $N = 40$ ), which did not differ from males captured at flowers ( $\bar{x} = 1.23 \text{ mm} \pm 0.042$ ,  $N = 40$ ) ( $t$ -test,  $t = 1.64$ ,  $P > 0.11$ ). Some males marked at the nest

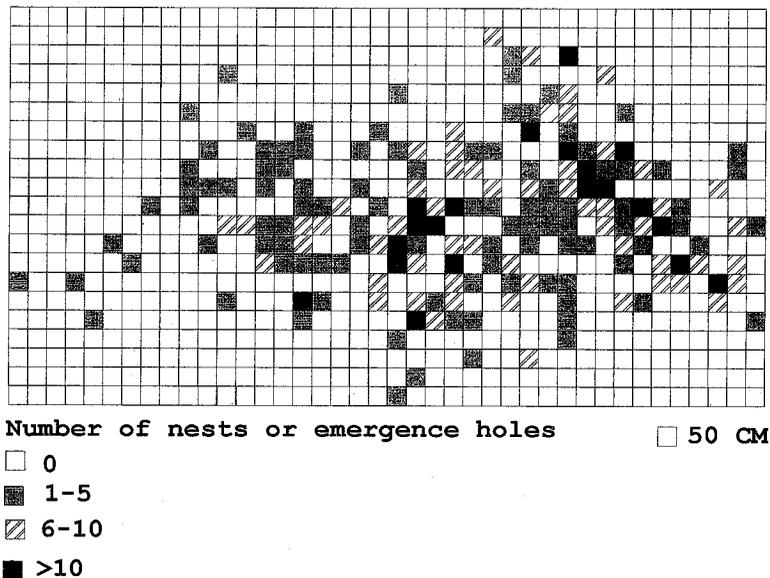


Fig. 2. Density map of a patch within an aggregation of *Calliopsis hondurasicus*.

site were also observed feeding at flowers ( $N = 13$ ), suggesting that these different behaviors may simply be feeding opportunities, and not a reflection of alternative mating strategies.

At the nest site, males patrol a well-defined area with a regular route, returning repeatedly to one or several perch sites—a rock, a stick, or rarely vegetation (Fig. 1). They chase conspecific females and males that enter the territory, and occasionally other flying insects. During 10-min periods in which males encountered conspecifics, on average a male had 6 interactions with males ( $\bar{x} = 6.04 \pm 2.85$ ,  $N = 20$  periods) and 2.2 interactions with females ( $\bar{x} = 2.19 \pm 1.72$ ,  $N = 21$  periods). Males in pursuit of females flew differently than males in pursuit of other males. In the latter, a male flew rapidly and quickly intercepted the other male. In contrast, a male in pursuit of a female shadowed or trailed after her approximately 5–10 cm away. An intruding male either immediately left the territory [61 of 92 (~67%) male-male interactions], or the two males engage in what Shinn (1967) termed a “spiral flight” for *C. andreniformis*. In these spiral flights two males face each other at a distance of less than one or two body lengths, often jostling one another and flying rapidly in an ever-tighter, vertical spiral, climbing to more than 1 m above the ground. Each flight lasts less than several seconds, but I could not reliably time their duration. During approximately half of the flights ( $N = 17$  of 31), the pair tumbled and crashed to the ground, presumably because one male grabbed hold of the other. On the ground they wrestled, and often bit one another on the legs. In the remainder of the flights the intruder flew away at the end of the spiral flight. In almost all cases ( $N = 26$  of 31 flights, ~84%) the intruder eventually flew away. In 5 cases the intruder successfully evicted the territory owner, and took up residence. The mean body size of these winners ( $\bar{x} = 1.25 \text{ mm} \pm 0.019$ ,  $N = 5$ ) was not different from the evicted losers ( $\bar{x} = 1.26 \pm 0.022$ ,  $N = 5$ ), but small samples preclude statistical analyses.

Males that were collected to be marked returned immediately to their territory in almost all cases ( $N = 53$  of 63). Forty-two (79%) marked males were observed on the same territory on at least one subsequent day during the first week of activity, and one male was sighted on the same territory 9 days after marking (number of days between marking and last confirmed sighting on the territory,  $\bar{x} = 2.36 \pm 1.96$ ). In 15 cases, males were removed from their territories, and the next day these territories were occupied by other males (2 males were previously marked, but the other 13 were unmarked).

Nests and emergence holes of bees were patchily distributed within the aggregation (Fig. 2). At Kobbe, the areas where females emerged/nested consisted of three loose patches, each an exposed area separated from the others by grassy areas. Within a patch, larger males had larger territories (number of quadrats), but the relationship is marginally not significant ( $r = 0.40$ ; as a linear regression,  $F$ -ratio = 3.51,  $P = 0.077$ ,  $N = 20$ ). Similarly, larger males did not have territories with more emergence holes/nests ( $r = 0.34$ ; as a linear regression,  $F$ -ratio = 2.42,  $P = 0.137$ ).

Although males repeatedly pounced on females and attempted to mate, actual matings were rarely observed ( $N = 9$  out of  $>100$  pounces). Males mounted females from behind, and pulled at the females' wings with their front legs and mandibles. Mating was brief ( $\bar{x} = 92.7$  sec  $\pm$  22.69, for 6 complete copulations). In 3 cases mating pairs flew *in copula*. Apart from rhythmic thrusting with the abdomen and the biting movements described above, there were no other conspicuous copulatory or pre-copulatory courtship behaviors.

**FEMALE BEHAVIOR:** As with some other *Calliopsis*, females that were handled gave off a lemon odor [Shinn (1967) discusses possible functions]. Female *C. (C.) hondurasicus* tend to nest within loose to dense aggregations (Fig. 2), although isolated nests can be found with diligent searching. Most nests contained a single female ( $N = 39$  of 43). Near the end of the foraging season (1996/1997), the number of cells per single-female nest was  $7.04 \pm 2.82$  ( $N = 27$ ). I never observed marked females digging or provisioning a second nest. In 4 cases two females provisioned the same nest, with a mean of  $12.25 \pm 2.22$  cells per nest. In each pair, both females had developed ovaries and were mated, and both had well-worn wings, suggesting they were from the same cohort and both were breeding.

The nest architecture of *C. (C.) hondurasicus* does not differ from *C. (C.) andreniformis* illustrated by Shinn (1967). If there was no rain, nest entrances were surrounded by a mound of soil (up to  $\sim 30$  mm-diameter) thrown up during excavations. The loose soil usually filled the entrance and upper part of the tunnel. Nests consist of a single entrance that begins at a slight angle to the soil surface, and usually continues straight down to a depth greater than 4–5 cm, where the first cells are dug. The slightly constricted entrance has a mean diameter of  $3.6 \pm 0.33$  mm ( $N = 19$ ), opening into a larger tunnel with a diameter of  $3.96 \pm 0.29$  mm ( $N = 18$ ) at 3 cm depth. The main tunnel is a vertical shaft, up to  $\sim 14$  cm deep, and usually terminates as a blind burrow beyond the depth of the cells. Cells are connected to the main tunnel by short, lateral tunnels, approximately 1–2 cm long, that are filled with soil, as shown for *C. (C.) andreniformis* (Shinn, 1967) and *C. (Calliopsis) pugionis* Ckll. (Visscher and Danforth, 1993). Each cell usually occurred singly at the end of a lateral tunnel, but in 5 nests two or three cells were found in a linear arrangement, as shown for nests of *C. (Hypomacrotera) persimilis* (Ckll.) (Danforth, 1990). The oldest cells are near the surface, being progressively younger with increasing depth;

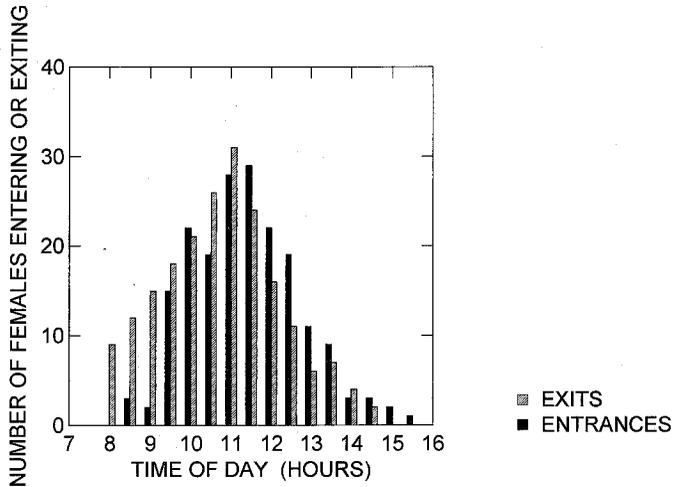


Fig. 3. Diel nest provisioning behavior in female *Calliopsis hondurasicus*. Black bars: females entering nests with pollen; gray bars: females exiting nests. Address all correspondence to W. C. Bailey.

most of them are less than 15 cm deep. The orientation of cells ranged from horizontal to an inclination of  $\sim 15^\circ$  relative to the ground, with the back end of the cell lower. Cells are elongate spheroids, and the entire inner cell walls are coated with thin, shiny secretions, except for the cell plug. The cell is sealed with an unpainted earthen spiral that is concave on the inner surface. The complete pollen ball is spherical and is coated with secretions, and the egg is placed atop the pollen ball.

Females began foraging at  $\sim 9:00$  A.M., and continued to do so until early afternoon ( $\sim 13:00$  P.M.), with a peak in late-morning (Fig. 3). Marked females made between 3 and 8 pollen trips per day ( $\bar{x} = 4.36 \pm 1.25$ ,  $N = 25$  females), which lasted from 10 to 110 min ( $\bar{x} = 37.83 \pm 19.92$ ,  $N = 81$ ).

In some nests, the first several offspring become adults during the same season, as inferred from the fact that i) nests excavated in late December and early January contained pupae in the uppermost cells, and ii) nests excavated at the end of the nesting cycle in late January and February had the uppermost two or three cells with obviously old, dried feces and filled with soil, while the other cells contained younger immatures (prepupae or late 4th instar larvae). The fate of these early emerging bees is unknown. Similar behavior occurs in *C. (C.) andreniformis*; Shinn (1967) stated that the overwintering generation in Kansas produces a generation of summer adults. In turn, these adults mate and produce another generation, some of which themselves become adults, and others remain as prepupae and overwinter.

Pollen samples from nest cells indicate that *Aeschynomene americana* (Papilionoideae) is the major resource for *C. (C.) hondurasicus* at this site; floral records of other Panamanian specimens are from *A. americana* (Michener, 1954). In central Panamá, *A. americana* flowers in the early dry season, from December to early February (Croat, 1978). Pollen availability may limit the seasonal activity of *C. (C.) hondurasicus*, since the weather in February and March is hot and clear, and other ground-dwelling bees continue to actively provision cells at the same site (Wcislo,

unpubl. data). However, data on pollen utilization are needed from other localities to confirm whether *C. (C.) hondurasicus* is a pollen specialist (oligolectic), as suggested by Michener (1954).

No *Holcopasites* (Hymenoptera: Apidae) cleptoparasitic bees have been observed at any of the *Calliopsis* aggregations in Panamá, and there was a remarkable absence of enemies at the site. Mutillid wasps of the correct size class were observed at the site, but there was no evidence that they successfully parasitized cells.

#### Discussion

**MALE BEHAVIOR:** The behavior of male *C. (C.) hondurasicus* is similar to behavior described for *C. (C.) andreniformis* in Kansas, in that males defend areas where females are emerging and nesting (Shinn, 1967). In contrast, at a small aggregation of *C. (C.) andreniformis* in Arizona, Rozen (1967) reported that few males were observed patrolling at the nest site, and no males attempted copulation there, while numerous males patrolled among nearby flowers. Males of *C. (Calliopsima) pugionis* fly near the surface over nest aggregations, but apparently do not establish or defend territories (Visscher and Danforth, 1993). These differences may relate to the high nest density at some *C. pugionis* aggregations, which are estimated to sometimes have more than 500 nests per m<sup>2</sup>. Further studies are needed to determine if *Calliopsis* males facultatively adjust their mate-searching behavior in response to local variation in female abundance.

**FEMALE BEHAVIOR:** The nesting behavior of female *C. (C.) hondurasicus* is also similar to behavior described for *C. (C.) andreniformis* (Shinn, 1967) and other *Calliopsis* (Rozen, 1967; Danforth, 1990). In general, *Calliopsis* are solitary bees, although a low percentage of nests of *C. (C.) hondurasicus* are provisioned by two females, and one such example is known for *C. (C.) andreniformis* (Shinn, 1967).

*C. (C.) andreniformis* produce an average of 3.4 cells/nest and each female customarily makes two nests according to Shinn (1967:918). Thus, overall productivity is 6.8 cells/female, similar to *C. (C.) hondurasicus*. Unlike *C. (C.) hondurasicus*, female *C. (C.) andreniformis* effectively distribute maternal investment among nests, as do some other aculeate Hymenoptera (e.g., Evans, 1965; Weislo et al., 1985). Such "bet-hedging" behavior hypothetically reduces the risk of catastrophic loss due to parasitism or nest destruction (reviewed in Seger and Brockmann, 1987).

Extreme host specificity (oligolecty) can greatly constrain the number of generations per season (Weislo and Cane, 1996). *C. (C.) andreniformis* visits at least 26 plant species from 12 families for pollen (Shinn, 1967; also Robertson, 1928). This flexibility in pollen preferences may help explain why *C. (C.) andreniformis* can have more than one generation per year. In contrast, *C. (C.) hondurasicus* apparently has a single generation per year. Data from more locations are needed to assess whether *C. (C.) hondurasicus* females are constrained by pollen availability.

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