Female Size and Nest Defense in the Digger Wasp
Cerceris fumipennis (Hymenoptera: Sphecidae: Philanthinae)

ULRICH G. MUELLER,[1] ALAN F. WARNEKE,[2] T. ULMAR GRAFE,[1]
AND PETER R. ODE[2]

ABSTRACT: An aggregation of the philanthine wasp *Cerceris fumipennis* Say was observed during nest-founding from March 25–31, 1989, at the Archbold Biological Station, Florida. Newly emerged wasps were individually marked and measured for head width. Observations of 35 nests over six daily activity periods revealed frequent nest switching and nest usurpation. Larger females displaced smaller females from their nests, and larger females maintained residence longer than smaller females. As a consequence, the average size of females holding a nest increased significantly during the nest-founding phase, but the average size of all females observed at the nest aggregation did not change during the same period. Size therefore predicts a female wasp's likelihood of acquiring and retaining a nest, suggesting that large females are competitively superior to small females during nest-founding. In some cases, two females appeared to share a nest, but did not provision simultaneously.

Nest switching and nest usurpation by conspecific females are common and widespread behaviors among sphecid wasps (Evans, 1973; Miller and Kurczewski, 1973; Brockmann and Dawkins, 1979; Elliott, et al., 1986; Alexander, 1986; Pfennig and Reeve, 1989). In the philanthine genus *Cerceris,* for example, nest switching has been reported for almost all species studied and seems to result, in some cases, from nest usurpation involving aggressive interactions between females (Alcock, 1975, 1980; Salbert and Elliott, 1979; Elliott et al., 1981; Evans and Hook, 1982a, b, 1986; Elliott and Elliott, 1987; Hook, 1987). However, none of these studies investigated the factors influencing a female's ability to usurp or defend a nest. We examined one such factor, relative body size, and its role in determining the outcome of competitive interactions among conspecific females during nest-founding in a population of *Cerceris fumipennis* Say.

C. fumipennis typically nest in compacted, sandy soils. Nests consist of a main burrow with several short side burrows, each terminating in a cell 10–20 cm below the surface (Evans, 1971; Kurczewski and Miller, 1984). Wasps emerge from cells more or less synchronously in spring or early summer. Females then acquire a nest by either reactivating the natal nest, usurping another female's nest, or digging a new one. Nests are provisioned with paralyzed buprestid beetles. When prey sufficient to fill a cell have been brought to the nest, the female places the prey in a cell, deposits an egg on the venter of the uppermost prey, and seals the cell (Kurczewski and Miller, 1984). As in other solitary wasps, the egg hatches after several days and the larva feeds on the paralyzed prey. Following winter diapause, adult wasps emerge from their cells in spring to mate and begin nesting.

[1] Field of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA.
[2] Field of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853, USA.
Corresponding author: Ulrich G. Mueller, Section of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, New York 14853, USA.

Materials and Methods

We observed a population of *Cerceris fumipennis* during the nest-founding phase from March 25 to 31, 1989. Nests were located in an area about 7 m × 11 m, 30 m north of Lake Annie, Archbold Biological Station, Lake Placid, Florida. Soil in the nesting area consisted of compact white sand with organic matter from lake sediments and burned vegetation. Vegetation in the nesting area ranged from none to scattered clumps of a decumbent grass. The study area was searched daily for ground-nesting Hymenoptera beginning March 20. The first females of *C. fumipennis* were seen the morning of March 25; thus, our study covered the first seven days of the nest-founding phase in 1989.

Over the course of the study period, 10 male and 87 female *C. fumipennis* were netted as they left their burrows or hovered in the study area. Particular attention was given to the capture of females. The size of each individual was estimated by measuring the maximum head width (HW) with dial calipers (Mitutoyo Model 505-633-50) to the nearest 0.05 mm. In sphecid wasps, head width is strongly correlated with body mass (O'Neill, 1985; Evans and O'Neill, 1988). Twenty female wasps were measured twice, once by each of two investigators. The correlation between measurements provided an estimate of the reliability of the measurement procedure. In only two cases did the two measurements diverge by as much as 0.1 mm. The correlation between the two investigators' measurements was highly significant ($P < 0.0001$, $R^2 = 0.983$).

To facilitate marking, each wasp was placed in a restrainer composed of a small plastic tube closed at one end with a removable cap. A portion of the cap had been cut out and replaced with a metal grid having a mesh size (about 3 mm) slightly smaller than the intertegular width of *C. fumipennis*. The tube was stuffed with a cylinder of soft foam-rubber such that a wasp could be immobilized between the foam and the metal grid, at the same time exposing the wasp's mesoscutum and abdominal terga for marking. Wasps were code-marked with unique color combinations of Testors® enamel, one dot on the scutum and a second dot either just behind the first on the scutum, or on the abdominal terga. After the enamel dried, wasps were released from the restrainer at the site of capture. Of 10 male and 87 female *C. fumipennis*, 4 (40%) and 74 (85%), respectively, were seen at least once after release. However, most of our analyses are based on 49 females that were observed in the study area for at least two days. Wasps are identified hereafter by their color codes (e.g., YG = yellow-green).

The activity of marked wasps was monitored daily by recording their behavior at or near nest entrances throughout the wasps' activity period. More than 450 nest-hours of observation yielded longitudinal records for individual wasps and individual nests. Generally, individual wasps could be identified by their markings when in slow flight or when entering nests. Females were generally active above ground between 0900 and 1600, though we saw active wasps as early as 0820 and as late as 1738. To determine which wasps were residents, a clear plastic cup was inverted over each nest entrance between 0700 and 0800 each morning, before wasps left their nests. The wasp or wasps emerging from a nest and caught in these cups were considered the residents of the nest. Wasps that spent the night in the top 2–4 cm of the nest entrance, above the sand plug put in place each afternoon by the resident wasp, were not counted as residents. To identify such non-residents, all nests were inspected before placing a cup over the entrance. To

facilitate simultaneous observation of several nests during the wasps' activity period, the cups were intermittently placed over individual nest entrances, allowing wasps to exit their nests and hover inside the cups, or to find their nests and hover outside the cups. Wasps attempting to leave or enter a nest were then identified and permitted passage by temporarily removing the cup from the nest entrance.

Voucher specimens of wasps, prey and parasites are deposited in the Cornell University Insect Collection, Lot no. 1187.

Results and Discussion

SIZE OF WASPS: Figure 1 presents the size frequency distributions of head width (HW) measurements for male and female *C. fumipennis*. Most strikingly, females showed substantial variance in HW and thus overall body size. The average HW of females and males was 4.432 mm (SD = 0.288, n = 87) and 3.364 (SD = 0.189, n = 10), respectively, and females were significantly larger than males (t = 9.587, d.f. = 95, P < 0.0005). Among females, size was not correlated with day of first capture during the study period as determined by linear regression analysis (F = 0.701, d.f. = 85, P > 0.25), suggesting that female size is not correlated with emergence date during the founding phase.

PROVISIONING: During our study, nests were provisioned with six species of buprestid beetles: *Buprestis decora* Fabr., *B. maculipennis* Gory, *Chrysobothris femorata* (Olivier), *Chrysobothris* sp., *Dicerca punctulata* (Schönherr) and *Agrilus lateralis* (Say). *A. lateralis* and *B. decora* have not previously been reported as prey of *C. fumipennis* (Scullen and Wold, 1969; Kurczewski and Miller, 1984). The first five species are large, boat-shaped buprestids ranging in length from about 13 to 16 mm and from 5 to 6 mm in maximum width. *Agrilus lateralis* has a length of about 9 mm, but is parallel sided and only 2 mm wide. Wasps carried the five larger species under their bodies with the beetle's head forward and venter up, a position typical of some *Cerceris* (Byers, 1978) and other philanthine wasps (Evans and O'Neill, 1988). *C. fumipennis* appeared to use only its legs to hold the larger buprestids while in flight. In contrast, wasps clasped the smaller *Agrilus* sp. about mid-thorax with their mandibles.

Females approaching their nest with prey were frequently pursued by 1–3 small miltogrammine flies. These flies initially flew about 30–45 cm below and behind the wasp but then darted in quickly to larviposit on the prey when the female entered her nest. The position of the flies below and behind the female is curious. This position may afford them the best opportunity for larviposition or perhaps this is the wasp's "blind spot." When being pursued by flies, wasps sometimes aborted their approach and flew off, returning a few minutes later. We saw several successful larvipositions. In one case, the beetle was abandoned by the wasp at the nest entrance and was found to have three fly larvae on the abdominal venter.

NEST SELECTION: Behavior of female *C. fumipennis* included extensive searching for suitable nest sites, nest switching, and usurpation of occupied nests. We do not know if the frequent nest switching and usurpation are characteristic only of the nest-founding phase, during which our study took place, or if they are typical of the entire nesting period. Females without nests typically flew close to the ground, entered several burrows in succession for brief examination (5–20 sec), and probed entrances to ant nests and depressions at the bases of grass or under
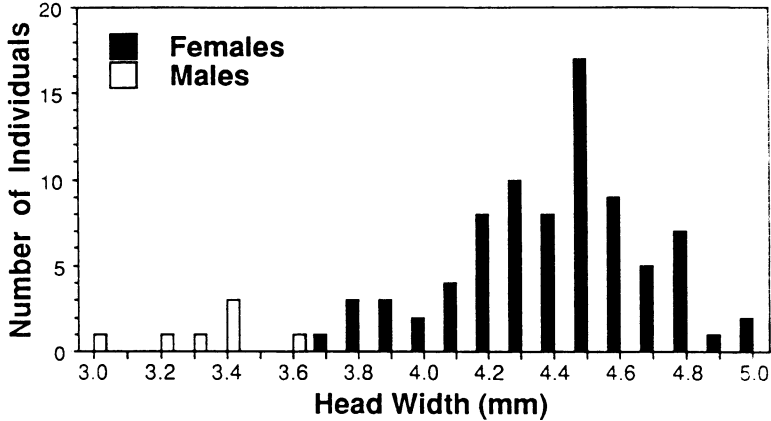
Fig. 1.   Size frequency distribution of male and female head widths in the wasp *Cerceris fumipennis* during the nest-founding phase March 1989.

pebbles. Excavations of new nests did not appear to be common, suggesting that most nests were reactivated. Thirty-five nests were regularly inspected and entered by wasps, but only 12 nests were observed to be provisioned during our study. Provisioning was observed first on March 27 and on all subsequent days.

Females were observed to inspect an average of 3.7 (SD = 1.9; $n = 49$ females) burrows per day. Because we did not observe individual females continuously, this figure underestimates the actual number of burrows they inspected each day. Larger wasps inspected significantly fewer burrows per day than did smaller wasps, as determined by regression analysis ($F = 6.04$, d.f. $= 47$, $P < 0.02$), suggesting that larger wasps either (1) restricted their search to fewer burrows, (2) selected and acquired nests earlier, and/or (3) occupied nests for longer durations before losing or abandoning them.

Although the onset of provisioning activity clearly indicated nest acquisition for those wasps in which it was observed, the exact time a wasp acquired a nest was frequently impossible to determine. For most wasps, spending the night inside the burrow was the only indicator that they had formed an association with a particular nest. Using this criterion of nest acquisition, the average size, measured by HW, of females successfully acquiring a nest for at least one day during the study period was significantly larger (mean HW = 4.53, SD = 0.209, $n = 41$) than the average size of "searcher" females (mean HW = 4.19, SD = 0.254, $n = 8$) that were unsuccessful in acquiring a nest ($t = 4.09$, d.f. $= 47$, $P < 0.0005$). Of the 41 females holding a nest, only 15 were observed to provision their nest. Females that were observed to provision during the study period were significantly larger (HW = 4.64 mm, SD = 0.203, $n = 15$) than all other females that had acquired a nest but were never seen provisioning (HW = 4.46 mm, SD = 0.180, $n = 26$) ($t = 2.92$, d.f. $= 39$, $P < 0.005$). Large females therefore were more likely than small females to acquire and provision nests during the early nest-founding phase.

NEST GUARDING AND NEST USURPATION: Females that were not nest holders spent much time inspecting and entering nests. An average of 6.46 (SD = 2.32;

range = 2.5 to 11.5) wasps other than the resident were observed to visit each of the 21 most closely watched nests per day. Visitation behaviors included landing and inspecting the nest entrance without actually entering, entering for varying lengths of time, and temporarily guarding the nest.

Frequent visitation by searching females may have forced residents to guard their nests against intruders. At nest 13, for example, yellow-green (YG) (HW = 4.95) successfully displaced the resident of the previous three days, red-copper (RC) (HW = 4.45), on the afternoon of March 30. The following morning, YG opened the nest and left the nest area, presumably to forage for nectar or prey. Within 2 minutes of YG's departure, RC entered nest 13 and went below ground for 50 minutes, finally returning to guard the nest entrance. Four minutes later, after 56 minutes away from the nest, YG returned to nest 13 without prey. The much larger YG then drove RC into the nest after a brief scuffle at the entrance. RC fled the nest 10 seconds later, tried to reenter, but was repelled by YG. In the next 40 minutes, YG repelled nine attempts to enter by five different wasps (all smaller than YG), including three more attempts by RC.

Unguarded nests were frequently usurped by females searching for a nest. Nest 16, for example, was provisioned by copper-green (CG) (HW = 4.55) on March 27 and held until the early afternoon of March 28, when copper-red (CR) (HW = 5.00) entered and plugged the nest in the absence of CG. Upon returning to the nest, CG unsuccessfully attempted to dig through the entrance plug, then abandoned its nest to inspect several other nests not in the immediate vicinity of nest 16. At nest 49, CG was confronted by red-yellow-blue (RYB) (HW = 4.45). Both grappled at the entrance, curving their abdomens forward apparently attempting to sting each other. CG then left and was not seen until the following morning when she emerged from nest 34, having spent the night in this nest. During the following three days, CG was unable to retain nest 34 or acquire a new nest, but repeatedly revisited its original nest (nest 16) among many others. At nest 16, CG was regularly confronted by CR, which guarded the nest almost for the entire day following usurpation, but began provisioning during late afternoon of that day.

In species in which disputes between males are resolved through physical combat, size is an important factor determining the outcome of intraspecific competition (Alcock et al., 1978; O'Neill, 1983, 1985; O'Neill and Evans, 1983; Evans and O'Neill, 1988). We therefore tested the hypothesis that individuals which displace resident females of C. fumipennis are larger than the displaced residents. For 45 nest takeovers observed during our study, head width measurements were known for both females. In 26 takeovers the resident was smaller, in 17 takeovers the resident was larger and in 2 cases there was no size difference. A one-tailed, paired t-test on the sizes of winners versus losers showed that usurping females were significantly larger than displaced females ($t = 1.78$, d.f. $= 44$, $P < 0.05$).

We also attempted to assess the importance of size in determining a female's capacity to defend her nest by comparing females that were residents for less than two days to females that held a nest for at least two consecutive days. The mean head width of females occupying the same nest for two or more days was 4.63 mm (SD = 0.191, $n = 16$), compared to 4.41 mm (SD = 0.240, $n = 46$) of females occupying a nest for less than two days. These means are significantly different ($t = 3.44$, d.f. $= 35.9$, $P < 0.001$). Although small in absolute terms, a difference

in head width of 0.22 mm represents a large difference in mass and presumably fighting ability, since small increases in a linear measurement such as head width translate into exponential increases in volume and hence body mass and strength (Evans and O'Neill, 1988).

The influence of body size on female nesting success is also apparent in the relationship between the average size of nest holders and time. If nests are scarce and costly to build, and if larger females are better at usurping and defending nests, then as more and more wasps emerge there should be a trend for the average size of residents to increase over time. As predicted, average resident head width was positively correlated with time during our period of observation as determined by regression analysis ($F_{1,3} = 86.5$, $P < 0.003$), while the average size of all females observed at the nest aggregation did not change during the same period ($F_{1,3} = 0.205$, $P > 0.6$; Fig. 2).

Several hypotheses have been set forth to explain the high frequency of nest switching and usurpation characteristic of some species of *Cerceris* (Alcock, 1975; Elliott et al., 1981; Hook, 1987). Tsuneki (1965) suggested that nest switching in *C. hortivaga* resulted from poor abilities to relocate nests. However, Alcock (1975) argued convincingly against this idea, and our own observations indicate that *C. fumipennis* can readily find nests even when the entrance and immediate surroundings are obscured and distorted by a plastic cup. A more plausible hypothesis is that, by usurping a nest, a female saves herself the time and energy needed to dig her own nest and may also acquire prey stored by the previous resident (Alcock, 1980). Several authors (Alcock, 1980; Kurczewski and Miller, 1984; McCorquodale, 1989a) have commented on the hardness of the substrates used by *Cerceris* for nesting. Such substrates increase the energetic advantage of usurpation. At our study site, the substrate consisted of dry, compact sand that may have made digging a time and energy-consuming task. A third hypothesis is that a female may choose to abandon her nest after provisioning one or a few cells in order to disperse her offspring in several nests, thereby decreasing the chance that all her offspring will be destroyed by predators, parasites, or natural disturbance (Alcock, 1975). This strategy would be less likely to evolve if a female had to dig each nest herself, given the time and energy costs associated with nest digging, and could explain, in part, the tendency for *Cerceris* to nest in aggregations.

NEST SHARING: A possible consequence of continual probing and attempted usurpation of nests is that two females will occasionally occupy the same nest simultaneously. Nest sharing is common in some species of *Cerceris* (Alcock, 1975, 1980; Evans et al., 1976; Evans and Hook, 1982a, b; Elliott et al., 1986; Hook, 1987; McCorquodale, 1989b, c) but rare or absent in others (Elliott et al., 1981; Evans and Hook, 1982b; Elliott and Elliott, 1987; Hook, 1987). During this study, two females of *C. fumipennis* co-occupied the same nest eleven times; eight times both wasps were marked, ruling out the possibility that one had just emerged from a cell in a reactivated nest. In one case three marked females were co-residents of a nest. However, none of these associations lasted for more than one day, and in none of these pairs did both wasps provision on the day they shared the nest. The observed incidences of co-occupation therefore may not represent true cases of nest sharing, defined as simultaneous provisioning by several females.

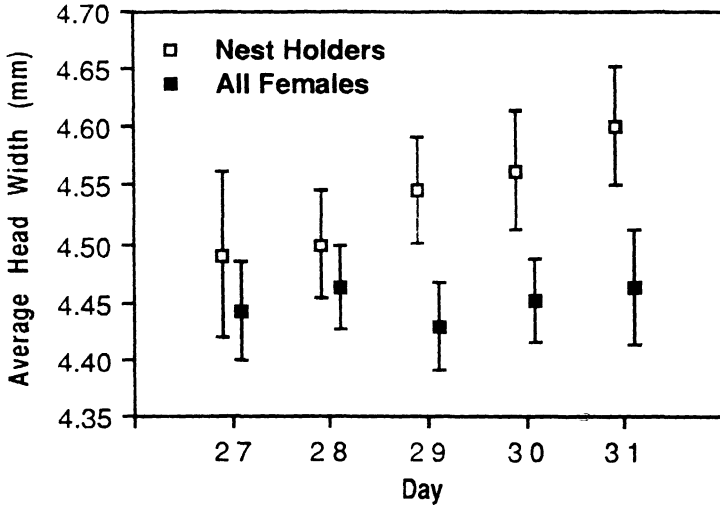Nest sharing may increase the reproductive success for both females if they are

Fig. 2. The average size (head width) of female nest holders and the average size of all females observed at the nest aggregation as a function of time (day) during the founding phase March 27–31, 1989. The increase in average size of nest holders over time is highly significant ($F_{1,3} = 86.5$, $P < 0.003$). The average size of all females present at the nest aggregation did not change during the same period ($F_{1,3} = 0.205$, $P > 0.6$). Error bars represent one standard error.

jointly more effective in deterring parasites, predators, or conspecifics attempting to usurp a nest. Nestmates have been observed to repel conspecific intruders in several species of *Cerceris* (Grandi, 1961; Evans et al., 1976; Alcock, 1980; Hook, 1987), and there is evidence that two or more females are better able to defend nests against predators, such as ants, and parasitoids, such as mutillids, than single females (Alcock, 1980; Evans and Hook, 1982b; Hook, 1987; McCorquodale, 1989b). On the other hand, it has been hypothesized that nest guards slow the entry of females carrying prey and thus increase the success of miltogrammine flies (Brockmann and Dawkins, 1979; Alcock, 1980; Evans and Hook, 1982b; Kurczewski and Miller, 1984). In addition, females sharing nests may provision at a lower rate than solitary females (Brockmann and Dawkins, 1979; Elliott et al., 1986). Willmer (1985a, b) has argued that smaller females are favored in hot climates and during unusually hot seasons as they are less likely to overheat. Willmer predicted that in species in which nest sharing is cooperative, one of the wasps should be "small" and its partner should be "large." The larger partner is a better forager because it can carry larger prey when the temperature is cool enough that it will not overheat. When the temperature becomes too high for the larger partner, Willmer hypothesizes, the smaller partner will be the better forager. Both will benefit from the additional nest defense a partner provides. For our limited record of nest sharing ($n = 9$) the average size difference between nestmates was 0.30 mm (SD = 0.113). However, in only three pairs was one member larger than the mean size (HW = 4.53 mm, SD = 0.209) of all nest-holding wasps, suggesting that the majority of individuals that shared nests were "small" wasps and would not complement one another in the way described by Willmer (1985a, b).

From this study it can be concluded that size is an indicator of female nest-

holding potential and determines, in part, the success of nest usurpation in *Cerceris fumipennis*. The following findings support this conclusion: (a) Female nest holders were larger than females that never obtained a nest; (b) the first females to provision nests were larger on average than non-provisioning nest holders; (c) nest usurpers were larger on average than the residents they displaced, leading to an increase in the average size of nest holders over time; and (d) wasps holding nests for two or more consecutive days were larger than wasps holding nests for less than two days.

In populations in which success in intraspecific competition is an important determinant of fitness and larger individuals are superior competitors, selection will cause an increase in size (Maynard Smith and Brown, 1986). In philanthine wasps, selection leading to increased size of females may act through several fitness parameters. First, ovarial egg size is correlated with body size, and egg size is likely to be correlated with larval viability (O'Neill, 1985). Second, the greater strength of large females enables them to carry larger prey, dig nests more readily (Evans and O'Neill, 1988) and, as suggested here, usurp and defend nests more effectively than smaller females.

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