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Parasitic and courtship behavior of *Phalacrotophora halictorum* (Diptera: Phoridae) at a nesting site of *Lasioglossum figueresi* (Hymenoptera: Halictidae)

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Abstract: Larvae of a phorid fly, *Phalacrotophora halictorum*, are parasites in the nests of a solitary sweat bee, *Lasioglossum figueresi*. Approximately 16% of 171 bee cells from 25 nests were parsitized by these flies Female flies copulated before attempting to enter host nests. Only if a bee was present, the fly was unable to enter the nest. After achieving genitalic coupling (intromission) a male fly apparently continued to court his mate by drumming his forelegs on her dorsum.

Key words: nest parasitism, courtship, phorid flies, solitary bees.

The biology of many of the natural enemies of bees and wasps is inadequately studied, despite the frequent assertion that these enemies play a significant role in shaping the social behavior of their hosts (Wcislo *et al.* 1988). This note describes the parasitic behavior of a fly, *Phalacrotophora halictorum* (Melander & Brues) (Diptera: Phoridae), which attacks the brood of a "solitary" bee, *Lasioglossum (Dialictus) figueresi* Wcislo (Hymenoptera: Halictidae). Information is also given on fly mating behavior, documenting post-intromission courtship involving structures other than the genitalia.

Phorid flies have diverse larval feeding habits, ranging from scavenging to endoparasitism, varying among and sometimes within species (Balduf 1928, Ronna 1936, Clausen 1940, Coyler 1952, Rychman 1953, Oldroyd 1964, Robinson 1971, MacDonald *et al.* 1975). Various species are associates of aculeate Hymenoptera, and there is little host specificity (Makino, 1985; Spradberry, 1973; Krombein, 1967; R. Edwards, unpublished checklist). This absence of specificity is probably not an artifact of poor taxonomic understanding of phorids, since individuals of the same species sometimes obtain food with alternative tactics (*e.g.*, Biegel 1953; McDonald *et al.*, 1975; for general discussions see Brues, 1936; West-Eberhard, 1986).

Phalacrotophora halictorum has a broad geographic range, from Brasil to the northern United States (Borgmeier 1963), and is catholic in its choice of hosts. It has been recorded from nests of many halictid bees, both social and solitary, including *Lasioglossum (Dialictus) pruinosus* (Melander and Brues 1903), L. *(D.) zephyrum* (Batra 1965, pers. obs.), *Agapostemon nasutus* (Eickwort and Eickwort 1969), *A. virescens* (Abrams and Eickwort 1981), and *Nomia melanderi* (Johansen and Mayer 1976). It has also been associated with *Perdita coreopsidis* (Andrenidae) (Danforth 1989), and a digger wasp *Lindenius columbianus* (Krombein et al. 1979).

MATERIAL AND METHODS

Observations were made between 15 January and 20 April 1986; 14 December 1986 and 28 May 1987; 10 December 1987 and 16 January 1988; and 30 May and 4 August 1988 at three nesting aggregations of *L. figueresi*, at about 1450 m, 1600 m, and 1800 m elevation, ca. 3 km south of San Antonio de Escazú, San José Province, Costa Rica (details in Wcislo, Wille, and Orozco, in prep.).

Flies were observed under natural conditions, usually with the unaided eye, although sometimes I used a hand-lens (10X). Flies were not individually marked. When appropriate, observations were timed (seconds) with a watch. Mean values are given with one standard deviation.

Nests were carefully excavated by blowing powder into the burrows and then digging up the contents. *Phalacrotophora* larvae and puparia were transfered to individual plastic containers and reared in the Laboratory Los Lirios in San Antonio de Escazú (elevation: ~1350 m). Usually it was not possible to unequivocally associate a puparium with an individual bee cell.

Voucher specimens of the adult bee and fly are deposited in Museo Nacional de Costa Rica (currently, Inbio, Heredia, Costa Rica) and the Snow Entomological Museum (SEM), University of Kansas; immature stages are in the SEM.

RESULTS

Synopsis of the hosts' biology

Most *L. figueresi* bees are solitary. Females usually nest in aggregations in vertical earthen banks along roads or trails. A typical nest has a central tunnel with lateral cells (Fig.1). The female provisions each cell with pollen and nectar, lays an egg, and then seals the cell with a soil plug. A cell may be open for up to several days (details in Wcislo *et al.*, in prep.).

Seasonal and diel abundance of flies:

Both adult male and female *P. halictorum* were present but not abundant at all three sites from December through early February. Adult flies were not found at other times of the year.

Flies were active between 9:00 and 14:30 on sunny or partly cloudy days. Males and females flew across the vertical bank, typically less than 5 cm from the surface. Individuals were easily sexed under natural conditions since males (length right wing: $\bar{x}$ = 2.78 ± 0.19 mm, n = 5) were noticeably smaller than females (length R wing: $\bar{x}$ = 3.46 ± 0.24 mm, n = 5). A crude index of fly activity was generated by hanging a 0.5 m long string in the middle of a nest aggregation where there were 23 bee nests/ 0.5 m^2; the number of female flies which crossed this string per 5 minutes was counted. For n=10 periods, the mean number of female flies per 5 minutes was 1.1 ± 0.99.

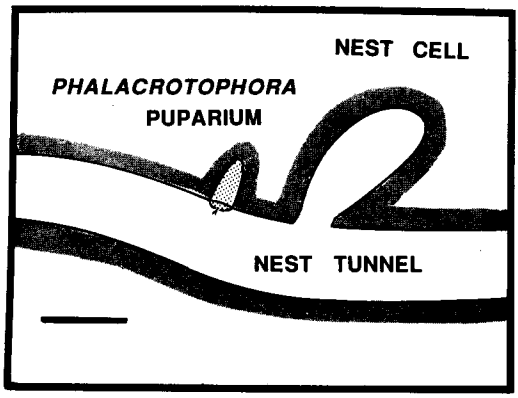

Fig. 1. Cross-sectional diagram through the soil of part of a nest of *Lasioglossum figueresi*, with a puparium of *Phalacrotophora halictorum* and a bee cell (mature nests have ~ 6-15 cells). Scale bar= 0.5 cm.

Male behavior

Males flew over the surface of the vertical bank, and frequently landed to inspect cracks in the soil, holes, and especially the nest entrances of *L. figueresi*. They ignored other males, and never entered nests; neither males nor females inspected "artificial nests" I bored into the soil. Eight of 11 (73%) complete copulations were initiated when a male met a female as she left a nest. One copulation began when a male approached a female as she sat on a nest-entrance turret, and two were initiated when males approached females that perched near nest entrances.

Female behavior

Females flew or walked erratically over the bank, and entered cracks, crevices, holes or bee nests. Usually (52 of 70 observations) females entered bee nests for less than 3 secs, and then re-emerged. In 21 of these 52 cases it was possible to see that a female *L. figueresi* was blocking the burrow inside the entrance. Ten times I tried to introduce flies (via plastic tubing) into occupied bee nests, and in all cases the fly's passage was blocked by the bee, which opened her mandibles and snapped at the fly. The flies all retreated into the plastic tubing.

After a quick exit from a nest (above) a fly either flew away, or perched near (< 2 cm) the entrance while facing it, as illustrated for *Phora* sp. (probably *Pericyclocera cata*, B.V. Brown, *in litt.*) by Melander and Brues (1903). The duration of such perching (excluding those lasting < 5 secs)

ranged from 12 to 121 secs ($\bar{x}$ = 34.8 ± 21.7, n = 22), and was much briefer than reported by others for this species. Melander and Brues (1903) observed a female that perched for "several hours", and Batra (1965) reported that females perched for "up to half an hour". Most flies (17 of 22) flew off following perching, while the remaining 23% re-entered the same nest.

Excluding the brief entries (T < 3 sec), females entered nests and remained inside from 7 to 17 secs ($\bar{x}$ = 12.2 ± 3.3, n = 18). Some of these females presumably oviposited, although I carefully excavated 10 nests following fly entry without finding any fly eggs (length = ~ 0.59 mm, based on dissections of females) or larvae. I was unable to ascertain how the parasite larvae gain access to the bees' cells.

Courtship:

The following descriptions are based on observations of 11 complete copulations (mean duration: x = 47.8 ± 6.9 secs), and numerous partial observations.

A male mounted a female without any preliminary courtship, and immediately inserted his genitalia. In no cases (n = 11) were males rejected before copulation. The female then took flight with the male *in copula;* he rode on her dorsum and did not use his wings. Similar flights have been noted for *P. halictorum* in Kansas (Batra 1965, pers. obs.) and Costa Rica (G.C. Eickwort per. comm.), as well as for some other phorids (Binns 1980, Sivinski 1988). In another phorid, males carry the apterous females (Miller, 1984). This first flight lasted up to 23 secs, although usually it was much shorter ($\bar{x}$ = 5.1 ± 6.0, n = 11). In a typical sequence the female takes flight and both fly over the nesting site, land and remain in the place for several seconds (T < 3), fly again, land, fly, etc., rarely covering a distance of more than 1 m in total. During the first 15-20 secs the male rapidly drummed his front legs, apparently striking the notum of the female's thorax. They were alternated left and right, in a manner somewhat similar to grooming the forelegs against each other. All males did this, at least while the pair remained on the bank.

After having paired for 11-24 secs ($\bar{x}$ = 18.4 ± 3.6), the female rapidly vibrated her abdomen up-and-down with a vigorous shaking movement, and then stopped. After several more seconds, she repeated this, with the cycle continuing for 14 to 39 secs until the pair separated. Females vibrated the abdomen both in flight and while on the bank. The function, if any, of this behavior is unclear. Males in *Phalacrotophora* have no true genitalic claspers (B.V. Brown, *in litt.*). Less derived phorids may possess such structures: the epiphallus may be inflatable in a related genus *(Gymnophora)* (Brown, 1987) and could lock the pair together when inflated.

After separating from the male, the female invariably entered a nearby nest of *L. figueresi*. This "mate then enter a nest" behavior has been noted in other populations of *P. halictorum* (G.C. Eickwort pers. comm. pers. obs.). The reasons for the repeated matings are unclear, although they are also known in other phorids (see Brown 1985, 1987, Miller 1984).

Nest parasitism

More than 250 nests of *L. figueresi* were excavated (Wcislo *et al.*, in prep.). Only those nests excavated in mid to late December contained larvae of *Phalacrotophora;* pupae were taken from nests excavated from February to May.

In 1987-88 (mid to late December) 25 nests were excavated specifically to look for *Phalacrotophora* eggs, larvae, or pupae. Larvae were found in six of these nests. These six nests had a mean of 5.2 cells each (s.d. = 0.75); there were on average 1.33 (s.d. = 0.52) parasitized cells/nest, each with x = 2.5 (s.d. = 0.54, n = 8 cells) fly larvae per cell. Phorid pupae were found in 13 nests (mean number of pupae per nest = 3.5 ± 1.5). Twenty-eight of 171 cells contained fly larvae, or were moldy and fly pupae found nearby. Larvae were found on the tops or sides of the pollen balls (see photograph in Johansen and Mayer, 1976). These pollen balls were considerably wetter than those in cells containing only bee larvae, and had a distinct odor of fermentation. Cells containing fly larvae always lacked bee larvae. Two larvae recovered from cells pupated in the laboratory 4 and 6 days after excavation, respectively.

As with some other flies parasitic in the nests of Hymenoptera (see *e.g.*, Wcislo, 1986), *P. halictorum* pupated away from the cell, presumably to avoid secondary fungal invasion of the cell. Puparia (length: *ca.* 3 mm) of these flies are flattened like a shield at the posterior end, which is flush with the wall of a tunnel in the nests of *L. figueresi* (Fig. 1); the remainder is inserted into the soil surrounding the tunnel. Young flies probably emerge into the tunnels of the nests of their hosts.

DISCUSSION

Fly parasites account for much lost productivity in the lives of bees (*e.g.*, Schmid-Hempel and Schmid-Hempel 1988, Schmid-Hempel *et al.* in press). *P. halictorum* were never observed entering nests in which an adult female was present, while they readily entered those from which a female was absent. Such observations highlight the presumed importance of nest defense (Lin and Michener 1972). The incidence of parasitism in this study of solitary bees (16% of 171 cells from 25 nests) is within the range of rates reported for other bees and wasps. Simões *et al.* (1980), for example, report that a mean of 9.7 % (range: 0-37%) of cells in colonies of eusocial *Scaptotrigona* stingless bees were parasitized by phorids. Approximately 6% of larvae of a social halictine bee, *Halictus ligatus*, were killed by bombyliid flies (Packer 1988).

The proximate mechanisms used by female *P. halictorum* to locate and recognize host nests are unknown. Females are probably attracted by visual cues, although they never entered artificial holes bored into the soil. Other flies use a combination of both visual and olfactory cues (Wcislo 1986).

Although comparative data for other *Phalacrotophora* are not available, the extended post-coupling male mating behavior of P. *halictorum* lends support to recent ideas on the evolution of courtship behavior and associated structures (Eberhard 1985, in preparation). According to this view, male courtship behavior continues after genitalic coupling, and functions to induce a female to perform certain reproductive behaviors which increases the liklihood of her using that male's sperm. In *P. halictorum* it is unlikely that this post-coupling behavior represents grooming, or has no function, since all males always performed it in a sexual context, and similar sorts of leg movements have been observed during post-intromission courtship behavior in other flies (*e.g.* Spieth 1954, Eberhard 1988). A well-studied example is the phorid, *Puliciphora borinquensis* (Miller 1984), in which a male rapidly drums the female's head or thorax with his forelegs. In some other phorids there is no apparent post-coupling courtship (*e.g.* Brown 1985, Sivinski 1988).

RESUMEN

Las larvas de la mosca *Phalacrotophora halictorum* actúan como parásitos en los nidos de la abeja solitaria *Lasioglossum figueresi*. Aproximadamente, 16% de 171 celdas en 25 nidos contenían el parásito. Las moscas hembras copulan antes de intentar entrar en los nidos, lo cual no logran únicamente si hay alguna abeja. Luego de la penetración el macho aparentemente contínua cortejando a su compañera, tamborileando las patas delanteras sobre el dorso de ella.

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