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Invasion of Nests of *Lasioglossum imitatum* by a Social Parasite, *Paralictus asteris* (Hymenoptera: Halictidae)

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WCISLO, W. T. 1997: Invasion of nests of *Lasioglossum imitatum* by a social parasite, *Paralictus asteris* (Hymenoptera: Halictidae). *Ethology* 103, 1—11.

Abstract

Paralictus asteris Mitchell is a socially parasitic sweat bee that invades nests and becomes the dominant reproductive in colonies of a phylogenetically related host, *Lasioglossum (Dialictus) imitatum* (Smith). The parasite has a greatly enlarged quadrate head, with elongate scythe-like mandibles, and other morphological modifications apparently associated with a parasitic lifestyle. Nevertheless, the parasite did not forcefully enter nests. Host guards adopted a defensive posture at the nest entrance when they contacted a dead, frozen parasite, suggesting that they recognized the intruders as parasites. Living parasites, however, only sometimes induced this guarding response, while in other cases parasites entered host nests without obvious signs of aggression from the guard. Guards also responded aggressively to both frozen and living conspecifics from other nests, but were not aggressive to living or frozen nest-resident conspecifics, suggesting that the cues used for recognition of both unrelated conspecifics and parasites are chemical ones. More than one parasite can invade and occupy a nest, and successful invasion was not influenced by whether a parasitic female was mated or had developed ovaries.

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Introduction

The evolution of sociality poses well-known problems to evolutionary biologists (e.g. DARWIN 1859; WILSON 1975; TURILLAZZI & WEST-EBERHARD 1996). Social behavior itself creates opportunities for cheaters or parasites (WCISLO 1989; ODLING-SMEE et al. 1996), but social parasitism has received much less attention than it deserves (e.g. HAMILTON 1971; WCISLO 1987). A social parasite enters a host nest, either kills or dominates the major reproductive ("queen"), and exploits host workers to rear her offspring (see, e.g. WCISLO 1987; HÖLLDOBLER & WILSON 1990). Obligate, interspecific social parasitism has evolved repeatedly in Hymenoptera (WCISLO 1987, 1989; HÖLLDOBLER & WILSON 1990; CARPENTER et al. 1993) and is hypothesized to originate via facultative, intraspecific parasitism (WEST-EBERHARD 1986; WCISLO 1987, 1989;

FIELD 1992; BROCKMANN 1993). Social and parasitic behavior has evolved repeatedly among sweat bees (Hymenoptera: Halictidae) (reviewed in WCISLO, in press), which have an astonishing array of behavioral variation both among and within species (e.g. MICHENER 1990; PACKER 1993; WCISLO, in press). Hence, sweat bees are excellent for studying the evolution of parasitic and social behavior.

Traditional taxonomies often place social parasite species in genera different from those of their hosts, obscuring phylogenetic affinities. This study, for example, concerns a parasitic *Paralictus* that utilizes a host in *Lasioglossum* (*Dialictus*). Separation of *Paralictus* s. str. from *L. (Dialictus)*, however, is not presently justified on morphological bases (W. T. WCISLO unpubl. data), nor on preliminary molecular studies (B. N. DANFORTH, pers. comm.). *Paralictus* is probably best included within *L. (Dialictus)*, from which the parasites probably evolved. Similar examples are known in the socially parasitic paper wasps (Polistinae, CARPENTER et al. 1993) and bumble bees (Bombini, WILLIAMS 1994). These close phylogenetic relationships between host and parasite lineages support MÜLLER's (1872) general hypothesis that lineages of social parasites are derived from their host lineages (reviewed in WCISLO & CANE 1996).

Social parasites overcome host defenses using tactics that range from brute force to chemical manipulation (e.g. FISHER 1984), comparable to the range of behaviors used by queens to gain reproductive dominance within a colony (e.g. WILSON 1971; MICHENER 1974; HÖLLDOBLER & WILSON 1990). Here, I address whether a socially parasitic sweat bee, *Paralictus asteris* Mitchell, uses aggression or passive chemical manipulation to enter nests of its host, *Lasioglossum (Dialictus) imitatum*. *Paralictus asteris* is a small bee (body length 4–5 mm) that has been reared from nests of the equally small *L. (D.) imitatum* (Smith) in New York (this study) and Kansas (MICHENER & WILLE 1961; W. T. WCISLO unpubl. data). One obvious external feature of female parasites is a greatly enlarged, quadrate head with elongate scythe-like mandibles, which taper to sharp points (W. T. WCISLO unpubl. data; MICHENER 1978). Internally, the head is filled with massive mandibular muscles. Analogous morphological modifications are often present in parasites that forcefully take over host nests (see MICHENER 1978; WCISLO 1987; HÖLLDOBLER & WILSON 1990; CERVO & DANI 1996). Such parasites often have coarsely punctate exoskeletons for defense. However, surface sculpturing of *Paralictus* is delicate (W. T. WCISLO unpubl. data; MICHENER 1978), as true for some other halictine social parasites (e.g. *Microsphecodes*, EICKWORT & EICKWORT 1972). Thus, *P. asteris* has some morphological traits that suggest aggressive behavior, yet has others that do not.

In addition to describing nest-entering behavior by the parasite, I also document parasitism rates by *P. asteris*, and include comparative data from an undescribed *Paralictus* species that was reared from nests of *L. (D.) versatum* (see MICHENER 1966 for the host biology).

Natural History Overview of the Host, *Lasioglossum (Dialictus) imitatum*

Lasioglossum (Dialictus) imitatum is a ground-nesting bee that is abundant in eastern North America. The life-history of the New York population is similar to well-studied populations in Kansas (as *L. inconspicuum*; MICHENER & WILLE 1961), except that the New York population has a shorter active season and has nests with fewer bees (G. C.

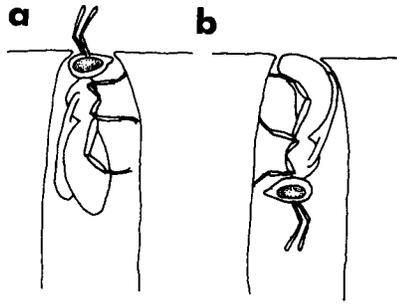


Fig. 1: Nest guarding by a female *L. (D.) imitatum*. (a) Position of nest guard, showing the restricted opening at the nest entrance. (b) Bee in a C-posture defensive position

EICKWORT unpubl. data, from field notes in my possession; W. T. WCISLO unpubl. data). Each nest has a circular entrance (diameter 1.3–1.5 mm) slightly larger than the diameter of the heads of the resident host bees (Fig. 1a). A vertical main tunnel descends into the soil and usually branches. Each cell is excavated from the side of these branches (illustrations in MICHENER & WILLE 1961), and a cache of pollen and nectar is placed in each cell as food for the developing offspring. An egg is laid on the stored food, and the cell is closed with soil, after which the adults probably do not interact with the immatures.

Mated adult host females overwinter in the soil. They emerge the following spring in late May to establish new nests and provision a small number (ranging from one to seven in New York) of mostly female-producing cells during Jun. (the 'pre-worker phase') (Fig. 2). They then stop foraging and wait for their brood to emerge. Offspring emerge in early Jul., and most of these Jul. emerging females work in the natal nest (the 'worker phase'). Worker-phase colonies have up to 11 foraging bees, so cell-provisioning rates are faster than during the pre-emergence phase, when only the foundress is gathering pollen. Consequently there are more host cells suitable for parasitization in worker-phase nests. During the worker phase each nest has a bee guarding the entrance. A guard usually excludes unfamiliar conspecifics and heterospecifics by blocking the entrance with her head (Fig. 1a) or metasoma (Fig. 1b). The guard allows nestmates to enter or exit by taking a few steps backward.

In Aug. males and females are produced that emerge and mate. Only the mated females overwinter, and the males eventually die at the end of summer. I performed the manipulations described below in Jul. and Aug., after worker emergence.

Methods

Study Site

Parasite–host interactions were studied during two summers (1993–94) in an aggregation (3 × 35 m) on a gently sloping (< 10°), north-facing, bare, earthen bank of a water filtration pond on the Cornell University Plantations (Ithaca, Tompkins Co., New York). There were ≈ 180 nests in 1993 and 155 nests in 1994. Nest density varied from one to 18 nests/m².

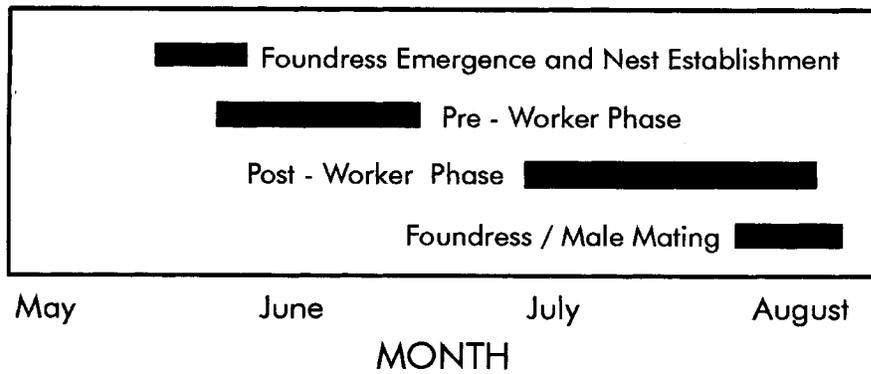


Fig. 2: Seasonal activity of the host, *L. (D.) imitatum*

Data on *Paralictus* n. sp. are from several aggregations of *L. (D.) versatum* in northeastern Kansas; these sites are described in MICHENER (1966).

Experimental Manipulations

Experiments involved three classes of test bees that were individually introduced to guard bees at the nest entrances of *L. (D.) imitatum*, as described below. One or 2 d prior to manipulations, I used a hand-held net to collect 'nestmate' bees that were returning to their nest after foraging. Nestmate bees were conspecific members of the same colony. Each nestmate was marked on the thorax with a colony-specific dot of Testor's color paint. Similarly, on the day of the manipulation, I collected 'non-nestmate' conspecifics. Each non-nestmate came from a different nest in an aggregation ≈ 30 m distant from the aggregation of nests where the tests occurred. Presumably non-nestmates were not immediate kin of the guards, nor of each other. I captured parasitic *P. asteris* while they were flying low (< 5 cm) over the nesting site, which is how they naturally search for nests to enter (W. T. WCISLO, unpubl. data), and marked each with a dot of color paint on the thorax.

Experiment 1: Responses of guards to simulated parasitism

Introductions of non-nestmates to guard bees at host nest entrances simulated attempted intraspecific parasitism, and introductions of parasites simulated attempted interspecific parasitism. Introductions of nestmate conspecifics provided baseline data. I sat near the entrance and placed a test bee into a clean 3-cm long, transparent plastic tube (inner diameter 3 mm), which was stopped at one end with a cork, and the other end with a pipe cleaner. I removed the cork and quickly placed the open end of the tube over the nest entrance, where I held it with my fingers. On occasion I gently prodded the bee using the pipe cleaner to start it moving toward the entrance, but usually the test bee moved freely toward the nest entrance. I used each nest only once to receive an introduced bee. To control for disturbance effects from placing a tube over a nest entrance, I placed an empty plastic tube on other nests and recorded the guards' responses. I analyzed treatments using the computer statistical package SYSTAT (WILKINSON 1989), but the manipulations were not blind, since I knew whether introduced bees were nestmates or non-nestmates, or parasites. After introducing a parasitic bee, I excavated nests as described below in order to determine whether or not the colony was already parasitized.

Guards responded in one of three ways when I introduced a test bee (Fig. 3). The guard could: 1. Admit the bee by stepping back and allowing it to enter the nest; 2. Aggressively attack by lunging at the stimulus with its mandibles making biting motions and curling the metasoma (abdomen) forward to sting the intruder; or 3. Turn around 180° and curl the metasoma in a 'C-posture' to block the entrance with the dorsal surface of her abdomen (Fig. 1b). A 'C-posture' occurs in many halictine bees as an escalated response to attempted invasion by natural enemies, including unrelated conspecifics (BELL 1974; BELL & HAWKINS 1974). Thus, guards may first display an aggressive response, and then block the entrance with a C-posture

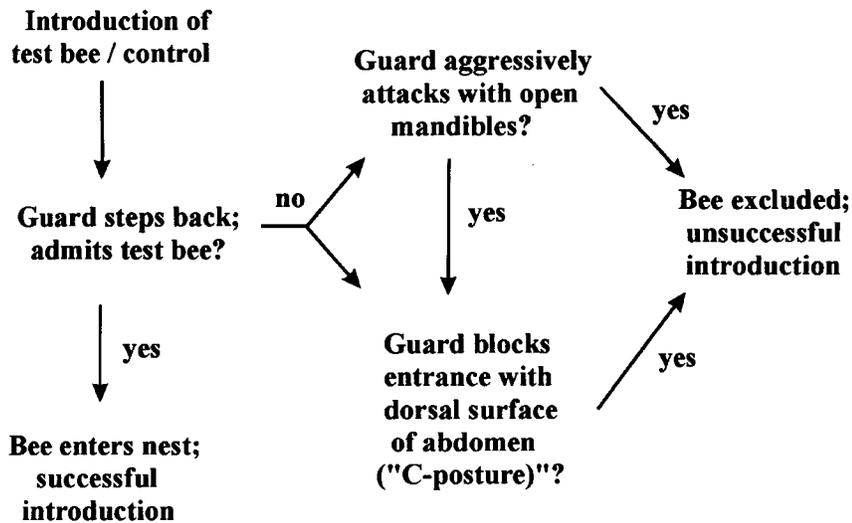


Fig. 3: Flow chart showing the possible responses of an *L. (D.) imitatum* guard bee to an introduction of a test bee, simulating intra- or interspecific parasitism

(Fig. 3), but these escalations were not included in the analyses. Guard bees remained in a C-posture from a few seconds to nearly 3 min. The length of time that the dorsal surface of the guard's abdomen was visibly blocking the nest entrance was recorded with a stopwatch to the nearest second.

Experiment 2: Cues used by guards to recognize parasitic bees

To determine the nature of the cues used by guard bees, I collected bees of the same three classes (parasites, and nestmate or non-nestmate conspecifics), transferred them individually to clean glass vials, and froze them in vials on dry ice. I kept bees frozen until they were used (up to 40 min). I introduced each one to a guard by gripping her right mid-leg with fine jeweler's forceps. I held the bee about 5 cm away from the nest and slowly moved the bee head-first toward the guard, as if she were flying towards the entrance, until the guard touched the introduced bee with her antennae, or showed some other behavioral response. Between trials, the forceps were washed with hexane. Empty forceps were introduced to guards to control for effects of approaching a guard with forceps. Responses of the guard bees were recorded as described above.

Experiment 3: Seasonal and social effects on invasion success

Once per week throughout each season I excavated nests to determine whether colonies were parasitized, and to obtain naturally parasitized nests to ascertain whether parasites were mated and reproductively active. Using a 20-cc syringe, I filled nests with liquid plaster of Paris early in the day when all the bees were in the nest. The plaster hardened, enabling me to trace the path of the tunnel accurately through the soil when I excavated the nest. Nest residents were removed from the plaster cast, placed in preservative, and later dissected to determine their mating and reproductive status.

Voucher Specimens

Voucher specimens of *Lasiglossum (Dialictus) umbripenne*, *P. asteris*, and *Paralictus* n. sp. are in the Cornell University Insect Collection (Ithaca), the University of Kansas Natural History Museum (Lawrence), and the Dry Reference Collection of the Smithsonian Tropical Research Institute (Balboa, Republic of Panamá).

Table 1: Responses of guard bees of *Lasioglossum (Dialictus) imitatum* to introduction of living bees and a control. Aggressive responses, Pearson's $\chi^2 = 79.7$, $df = 3$, $p < 0.0001$; C-posture, Pearson's $\chi^2 = 36.2$, $df = 3$, $p < 0.0001$

Manipulation (n)	No. of aggressive responses (%)	No. of guards adopting C-posture (%)
Non-nestmate, conspecific (50)	47 (94)	18 (36)
Nestmate, conspecific (20)	1 (5)	0 (0)
Parasite (35) ¹	4 (11)	13 (37)
Empty tube (20)	0 (0)	0 (0)

¹ Eighteen of these parasites successfully entered nests

Results

Experiment 1: Responses of Guards to Simulated Parasitism

Guards were aggressive in 94% of the attempted introductions of living non-nestmate conspecifics, while they were never aggressive towards living nestmates or controls (Pearson's $\chi^2 = 79.7$, $p < 0.0001$, $df = 3$) (Table 1). Following this initial aggression, living non-nestmates also elicited the defensive C-posture from the guard bee in over one-third of the attempted introductions, while nestmates did not elicit this behavior (Pearson's $\chi^2 = 36.2$, $p < 0.0001$, $df = 3$) (Table 1). Guards remained in a C-posture following exposure to a non-nestmate for a median time of 21.5 s ($n = 18$). Guards did not respond aggressively to an empty tube placed over the nest entrance, nor did they attempt to block the entrance in a C-posture (Table 1), indicating that the experimental protocol did not significantly influence their behavior.

The responses of guards to living parasites were highly variable. Parasites successfully entered host nests in over half (51%) of the introductions, while the parasites immediately induced an aggressive response (11%) or a C-posture (37%) in the other cases (Table 1). Of 17 unsuccessful introductions of living parasites, most times (76%) guard bees immediately adopted a C-posture in response to a living parasite, while they were aggressive the remainder of the times (Table 1).

Experiment 2: Cues Used by Guards to Recognize Parasitic Bees

Frozen non-nestmates elicited aggressive behavior by guards at the same level as did their living counterparts (Pearson's $\chi^2 = 0.543$, $p = 0.46$, $df = 1$), and frozen nestmates usually did not (Pearson's $\chi^2 = 77.7$, $p < 0.0001$, $df = 3$) (Table 2). These results show that chemical cues are sufficient to elicit an aggressive response. Frozen non-nestmates did not cause guards to assume a C-posture (Table 2), suggesting that the behavior of the introduced bee plays a role in eliciting this defensive posture.

In contrast, frozen parasitic bees usually (83% of 30 introductions) induced a guard to adopt a C-posture, without first biting at or otherwise behaving aggressively towards the parasite (Table 2). Moreover, in comparison to non-nestmates ($n = 18$), a guard bee remained in a C-posture for a longer time following exposure to a parasite ($\bar{X} = 58$ s, $n = 38$, pooled for frozen and living bees) (Mann-Whitney U test = 75.5, $p < 0.001$).

Table 2: Responses of guard bees of *Lasioglossum (Dialictus) imitatum* to introduction of frozen bees and a control. Aggressive responses, Pearson's $\chi^2 = 77.7$, $df = 3$, $p < 0.0001$; C-posture, Pearson's $\chi^2 = 120.0$, $df = 3$, $p < 0.0001$

Manipulation (n)	No. of aggressive responses (%)	No. of guards adopting C-posture (%)
Non-nestmate, conspecific (50)	45 (90)	0 (0)
Nestmate, conspecific (30)	1 (3)	0 (0)
Parasite (30)	5 (17)	25 (83)
Poke with forceps (40)	28 (70)	0 (0)

Experiment 3: Seasonal and Social Effects on Invasion Success

Of 18 parasites recovered from nest excavations and dissected successfully, 16 (89%) had sperm in their spermathecae. Of 26 parasites, 85% had developed ovaries, while 15% had slender ovaries, including the two parasites which were unmated. During experimental manipulations, eight of 18 (44%) parasites that successfully entered nests were mated. Likewise, 56% of the parasites that entered a nest had developed ovaries. These results suggest that mating and reproductive status are not associated with a parasite's ability to enter a nest. Similarly, nine of 11 ($\approx 82\%$) *Paralictus* n. sp. collected as they were entering nests of *L. (D.) versatum* had mated. In contrast to *P. asteris*, most female *Paralictus* n. sp. (three of 19 dissected, 15.7%) had slender ovaries. For both species, approximately half of the parasites entering nests had pollen in their crops (*P. asteris*: 10 of 18, 55.5%; *Paralictus* n. sp.: 11 of 19 females, 57.8%).

Mated *P. asteris* overwintered in the soil, and most became active when the host brood began to emerge in early Jul. During the pre-emergence phase parasites were rarely observed flying at the study site, and were infrequently found within *L. (D.) imitatum* nests (Table 3). By comparison, during the worker phase nests were frequently parasitized (Table 3).

Worker-phase colonies of *L. (D.) versatum* contained from nought to six adult *Paralictus* n. sp., with an overall parasitism rate of 67.7% (0% of six nests, Jul. 1964; 75% of 12 nests, Jul. 1957; 100% of six nests, Jul. 1954; and 100% of seven nests, Aug. 1957). There was no association between numbers of hosts and parasites per nest in this phase ($r = -0.02$, $p = 0.9$).

Nest excavations showed that the probability of a parasite successfully entering a host nest was independent of whether another parasite was already present in the nest,

Table 3: Percentages of *Lasioglossum imitatum* colonies parasitized by *Paralictus asteris*, before and after the emergence of workers. The number of excavated host colonies is given in parentheses

Year	% Host colonies with parasite	
	Pre-worker phase	Worker phase
1993	17 (18)	65 (25)*
1994	10 (20)	71 (17)**

* Between phases, $\chi^2 = 8.89$, $p < 0.005$

** Between phases, $\chi^2 = 7.14$, $p < 0.01$

Table 4: The relationship between the success of parasitic *Paralictus asteris* in entering a host nest, and whether or not that nest already contains a parasite. $G_{ADJ} = 2.31$, $p > 0.1$

Introduced parasite	Excavations	
	Parasite already present in nest	No parasite in nest
Enters nest	5	13
Is rejected	10	7

using a conservative G test adjusted for Yates' continuity (Table 4). Two parasites were found in each of six active New York nests, and up to seven parasitic females were found in inactive, late-season nests of *L. (D.) imitatum* in Kansas (W. T. WCISLO, unpubl. data). Twelve of 23 (52%) active nests of *L. (D.) versatum* contained more than one parasitic *Paralictus* n. sp.

Discussion

Attempts to enter host nests by parasitic *P. asteris* resulted in one of three outcomes: the guard bee either overtly attacked the parasite with its mandibles, blocked the nest entrance with the dorsal surface of the abdomen (a 'C-posture'), or allowed the parasite to enter the nest. If, however, a guard bee contacted a frozen parasite, then the guard usually blocked the entrance with a C-posture. Thus, chemicals provide guards with sufficient cues to recognize parasites. The guards also used chemical cues to recognize nestmates, as evidenced by the facts that they excluded living non-nestmates and were aggressive towards frozen non-nestmates, but were not aggressive towards nestmates. Studies of guarding responses by a congener, *L. (D.) zephyrum*, also showed that guards use chemical cues to learn the odors of familiar bees, and to discriminate between nestmates and non-nestmates (see MICHENER & SMITH 1987; GREENBERG 1988).

Do Parasites Physically Force their Way into a Host Nest?

The parasite may use several methods to enter nests, although brute force can be eliminated. In no case did the parasite use its enlarged head and elongate mandibles to force entry by killing the guard bee(s). Forceful entering, coupled with killing the host bees, is known in halictine parasites such as *Sphcodes monilicornus* (LEGWIE 1925) and other *Sphcodes* (see SICK 1990). The cephalic modifications of *Sphcodes* are not as pronounced as they are in *Paralictus* (see MICHENER 1978). Indeed, parasitic *P. asteris* were killed by guard bees of a non-host congener, *L. (D.) zephyrum*, following experimental introductions (W. T. WCISLO unpubl. data).

Do Parasites Chemically Manipulate their Hosts to Enter Nests?

Social parasites might enter nests by chemical manipulation or mimicry. A parasitic ant (*Polyergus*), for example, aggressively kills the host queen, from which it obtains chemicals which facilitate its integration into the colony (TOPOFF & ZIMMERLI 1993). Parasitic *Sphcodes pimpinellae* enter host nests of a social *Augochlora*, and immediately

afterwards the host bees all left the nest and flew or 'staggered' away (ORDWAY 1964). TENGÖ & BERGSTRÖM (1977) demonstrated that chemical profiles of host females were similar to parasitic males; they hypothesized that males pass the chemicals to female parasites during mating, which facilitate nest entry. Preliminary gas chromatographic analyses of *Paralictus-Lasioglossum* samples do not suggest chemical mimicry (W. T. WCISLO & H. FACUNDO, unpubl. data), but it is possible that active chemicals are released in small quantities or are released only during interactions with a guard, and would be undetected with our methods. *Paralictus* are rarely collected on flowers, so it is unlikely that they acquire any floral odor that facilitates nest entry, or that they contact other host bees and acquire their odor by adsorption.

Under laboratory conditions, non-nestmates of *L. (D.) zephyrum* can be introduced into a conspecific colony if they are less than ≈ 2 d old, while they are rejected if they are older (pers. obs.; see MICHENER & SMITH 1987). Halictine social parasites might exploit this discrimination system via chemical mimicry of newly emerged, reproductively immature bees. The ability of *Paralictus* to enter nests successfully, however, is unrelated to reproductive status (i.e. degree of ovarian development or whether or not a female mated). Thus, either parasites do not mimic reproductively immature host bees, or the parasites retain a putative 'immaturity' odor into reproductive maturity.

Do Parasites Exploit Host Kin Recognition Systems?

Based on studies of a congener, *L. (D.) zephyrum*, host bees probably learn the odors of nestmates, and use this information to discriminate against unfamiliar bees (MICHENER & SMITH 1987; GREENBERG 1988). Host bees in already parasitized nests would encounter newly enclosed adult parasites, and could learn odors of parasites as familiar bees (i.e. nestmates), rendering subsequent parasitism more probable (e.g. TOPOFF & ZIMMERLI 1993). It may be unlikely, however, that host sweat bees would generalize a learned response to other parasites, unless all parasites were identical with respect to putative recognition chemicals. LOTEM (1993) proposed that the potential costs of imprinting on a brood parasite select against brood-related learning capabilities in some passerine birds. If kin discrimination systems of sweat bees are generally based on learning the odors of individual nestmates, then they avoid this potential cost of imprinting on a parasite.

Are Substrate Vibrations used in Aggressive Signaling?

Substrate or airborne vibrations may play a role in immobilizing the guard bee, although these were not measured. Parasitic bumble bees (*Psithyrus*), for example, vibrate a set of flight muscles during dominance interactions, and these act as airborne sounds or substrate vibrations which cause some workers to become motionless (FISHER & WEARY 1988).

What is the Relationship Between the Parasite's Structural Modifications and its Behavior?

The parasitic bee, *P. asteris*, has morphological features indicative of physical aggression, yet does not forcefully enter host colonies. The cephalic modifications of

parasitic *Paralictus* may be used in combat with host queens within the nest. During nest excavations, however, no dead bees with body punctures were encountered (W. T. WCISLO unpubl. data). It is also possible that resident parasites use the structures in combat with conspecific parasites that subsequently attempt to invade the nest. If the latter is true, then it is difficult to explain why more than one parasite was found in some nests of both *L. (D.) imitatum* and *L. (D.) versatum*. By comparison, more than one adult female of the social parasite *Microsphecodes kathleenae* typically inhabit a single host nest at one time (EICKWORT & EICKWORT 1972), but this parasite's head is not greatly modified.

Conclusions

Guards exclude non-nestmate conspecifics and chemically recognize parasitic bees as enemies because they block the nest entrance when they contact a frozen parasite. Live parasites, however, are able to subvert the guard's discrimination system and enter nests. The mechanisms by which they achieve this result remain to be elucidated.

Acknowledgements

I am grateful to the late George EICKWORT, who showed me the nesting site and helped in many ways over many years. C. D. MICHENER generously provided unpublished data on another species, and D. CONLON helped with illustrations. For helpful criticisms on the manuscript, I thank J. BROCKMANN, J. CHRISTY, L. PACKER, D. ROUBIK, and an anonymous reviewer. These studies were supported by a National Science Foundation Environmental Biology Post-doctoral Fellowship (BSR-9103786). General research funds from the Smithsonian Tropical Research Institute supported manuscript preparation.

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Received: December 13, 1995

Accepted: May 8, 1996 (J. Brockmann)