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**Nest Localization and Recognition in a Solitary Bee,  
*Lasioglossum (Dialictus) figueresi* Wcislo  
(Hymenoptera: Halictidae), in Relation to Sociality**

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**Abstract**

Sweat bees [*Lasioglossum (Dialictus) figueresi*] returning to their nests were not disturbed if small-scale landmarks were added near nests before bees made orientation flights. Landmarks added after orientation flights delayed bees in locating nests when they returned. Spatially displacing landmarks had no effects on bees returning to their nests. Nest entrances usually had conspicuous turrets, but these were not required for nest recognition. Turrets provided some cues concerning nest identity since searching bees preferentially contacted their own turrets over alien ones. Swabbing the inner lining of a nest tunnel with hexane significantly delayed the bee's entry into the nest, but distilled water or an equal amount of hexane applied to the outside of the nest had no effect. The delay induced by a hexane wash was reduced significantly by placing the bee's unwashed turret on the nest entrance. Adding whole-body hexane extracts from probably unrelated females to nest entrances significantly delayed bees' entering nests.

A review of mechanisms for nest recognition within Apoidea shows that to date olfactory mechanisms are more prevalent among bees (Apiformes) than wasps (Spheciformes). This pattern may be an artifact of the little information available on wasps. If substantiated, then known cases of olfactory nest recognition generally co-occur with a tendency toward social evolution within Apoidea, supporting a hypothesis proposed by HÖLLDOBLER & MICHENER (1980).

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**Introduction**

Bees and other solitary, social or brood parasitic aculeate Hymenoptera have well-developed abilities for home-range and nest orientation (reviews by TURNER 1923; CHMURZYŃSKI 1964; VON FRISCH 1967; WEHNER 1981). Various authors have linked homing abilities to brood care, and to the repeated evolution of sociality in Hymenoptera as compared with other insects (e.g., WHEELER 1928; EVANS & WEST-EBERHARD 1970; WILSON 1971). Complex insect societies are held together in part by bonds of kinship (HAMILTON 1972), which are mediated by olfactory

cues (refs. in FLETCHER & MICHENER 1987). HÖLLDOBLER & MICHENER (1980) hypothesized that one evolutionary origin for kin-recognizing abilities may be olfactory nest recognition among solitary aculeates (also e.g., MICHENER 1982; BROCKMANN 1984; GAMBOA et al. 1986; MICHENER & SMITH 1987). Many people suggested that solitary bees use olfactory cues for nest recognition (e.g., LUBBOCK 1882; SHINN 1967), and several recent experimental studies support these suggestions (refs. in Table 5). No studies, however, involved solitary species in lineages with eusocial behavior.

In this paper I report experiments on visual and olfactory cues used for nest recognition by a solitary sweat bee, *Lasioglossum (Dialictus) figueresi* Wcislo, a relative of numerous species with eusocial behavior, including *L. (D.) zephyrum*, a species whose kin-recognizing abilities have been well-studied for both males and females (reviewed in MICHENER & SMITH 1987; GREENBERG 1988).

I also review nest-recognizing mechanisms within Apoidea. The superfamily Apoidea is generally regarded as a natural (monophyletic) group, consisting of the bees (Apiformes) plus some or all of the sphecoid wasps (Spheciformes) (MICHENER 1944; BROTHERS 1975; LOMHOLDT 1982). Among the > 400 genera of bees (R. ROBERT's unpubl. checklist, 1986) are numerous lineages having social and parasitic behavior (LINSLEY 1958; MICHENER 1974). In contrast, among the > 200 genera of spheciforme wasps (BOHART & MENKE 1976) these behavior patterns are rare (EVANS & WEST-EBERHARD 1970; EVANS & HOOK 1986). A prediction derived from the Hölldobler-Michener hypothesis is that olfactory nest-recognizing abilities should be wide-spread in solitary bees, and occur less frequently among related solitary wasps (WCISLO 1990b).

#### Synopsis of *L. (Dialictus) figueresi* Nesting Biology

Most *L. figueresi* were solitary bees (for details see WCISLO et al., subm.). Females dug tunnels in soil in vertical earthen banks, and provisioned excavated

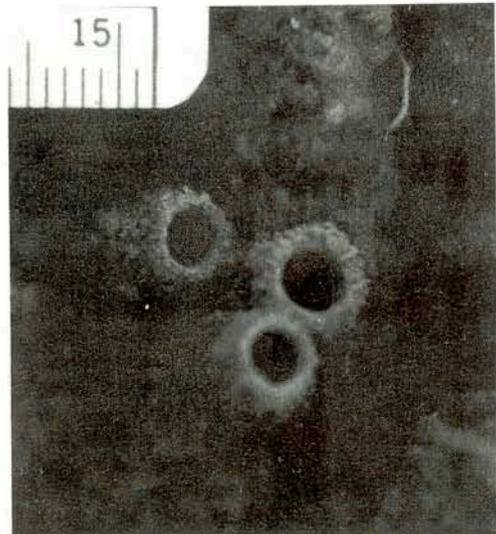


Fig. 1: Nest turrets of *Lasioglossum figueresi* females. All three nests were active at the time of this photograph. Each division on the scale bar: 1 mm

cells with pollen and nectar collected from flowers during foraging trips. Nest entrances were usually surrounded by chimney-like turrets, more or less perpendicular to the bank (Fig. 1; lengths of turrets: 0—25 mm). On sunny or partly cloudy days, females began flying at approximately 9.00 h, making between one and five foraging trips during each day of activity. Females made brief orientation flights each day before beginning to forage.

A close relative of *L. (D.) figueresi* is a eusocial bee, *L. (D.) aeneiventre* (WCISLO 1990a). Since nothing is known of their systematic placement relative to other *L. (Dialictus)*, it is possible that *L. (D.) figueresi* is secondarily solitary.

Voucher specimens of the bees and the nest turrets are in the Snow Entomological Museum, University of Kansas; additional vouchers of the bee are in the Instituto Nacional de Biodiversidad de Costa Rica (Santa Domingo, Costa Rica), and collections listed in WCISLO (1990a).

## Materials and Methods

### Study Site

Experiments were conducted from 25 Dec. 1985 to 8 Feb. 1986, and from 2 Jan. to 10 Feb. 1987 at two nesting aggregations of *L. figueresi* near San Antonio de Escazú, San José Province, Costa Rica. At "Estacion 9" more than 300 bees nested in a north-facing earthen bank (approx. 10 m long) on the road to the summit of Cerro San Miguel, passing through open pasture and agricultural fields. At "Near site" between 175 and 350 bees nested in a west-facing bank of an earthen road passing through agricultural fields. Within the "Near site" aggregation, no nests were farther than 55 cm from a neighboring nest, and most nests had nearest neighbor distances < 10 cm. Nearest-neighbor analyses are given in WCISLO et al. (subm.). At both sites there are fences, shrubs, and trees at the top of the bank, so many complex visual landmarks are available to the bees.

### Experimental Studies

Prior to experimental manipulations I individually marked bees on the thorax with dots of enamel paint. Females were used for single manipulations unless stated otherwise, and data are based on observations of pollen-laden bees returning to their nests on their first foraging trip of the day (unless stated otherwise). While making observations I stood at pre-determined stations to minimize any disturbances due to the bees using me as a landmark.

I timed observations with a watch, and quantified the following behavior:

"Duration of entry" is the duration (in s) from when a marked female first approached her nest (from 1 m away) to when she entered it. If a bee entered her nest directly, then a conservative value of 5 s was used; because of this truncated estimate, non-parametric statistics were used.

"Number of approach flights" is the number of approaching flights a female made before she entered her nest. An approach flight occurred when a returning bee passed above a mark on the ground (ca. 1 m from the bank) and flew to within < 10 cm of the nest entrance. A returning bee normally made one approach flight and then entered her nest. If there was some perturbation, the returning bee often briefly hovered (< 5 s) 1—5 cm in front of the bank, facing her nest; she then flew away and quickly returned to begin another approach flight. The shapes of the flight paths were not scored.

"Durations of entries" and "number of approaches" are given as medians with ranges. Comparisons were made using Mann-Whitney U tests, or Wilcoxon sign rank tests (SOKAL & ROHLF 1981); pertinent computer software was developed by R. ROGGERO (University of Kansas).

### Experiment 1: Visual Cues and Nest Localization

I placed objects near (~ 4 cm) nest entrances both before and after bees made orientation flights to determine if bees perceive visual cues and respond to their manipulation (cf. TINBERGEN 1972a).

These objects consisted of 6 wooden discs, each with a diameter of about 2.5 cm and a height of about 1 cm. Some were unpainted and some were painted white with a 5 mm black diagonal band. The objects were pierced with nails and placed in a circular formation (diameter = 8 cm) centered on the nest entrance (Fig. 2). During some preliminary trials I used a circle of 6 green coffee fruits, each of which was pierced with a pin and placed as described above; these trials gave similar results to those using wooden discs. (At least some bees have trichromatic vision with green color receptors; MENZEL et al. 1988.) I left objects in place for 6 to 9 d prior to further manipulations, which are described below. Unless stated otherwise, manipulations were made while bees were foraging.

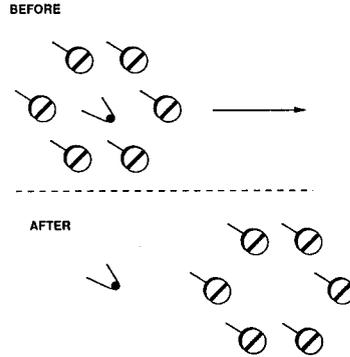


Fig. 2: Diagram showing six painted discs placed in a ring centered on the nest turret of *Lasioglossum figueresi*. A ring of six cues is left in place during a training period (top), and then shifted a given distance during an experimental trial

To determine if bees learn the positions of local landmarks during orientation flights, I presented cues prior to each bee's daily orientation flight ( $n = 39$  bees), and recorded their responses when they returned from foraging. Another 38 bees were allowed to make orientation flights, and depart to collect pollen. I then put cues in place, and scored the responses of returning bees.

To determine if the displacement of local landmarks caused bees to fly to where the landmarks were moved (cf. TINBERGEN 1972 a), I put objects in place before a bee made an orientation flight and departed. The cues and the bee's turret were displaced  $< 30$  cm to the left or right (determined by a coin flip) of the original position ( $n = 40$ ). Methods for turret displacement are described below.

### Experiment 2. Role of Turrets for Nest Localization and Recognition

a) *Removal of turrets*: I removed turrets from nest entrances while bees were foraging (cue deletion,  $n = 25$ ), and scored the responses of returning bees, in comparison with those of bees returning to unmanipulated nests.

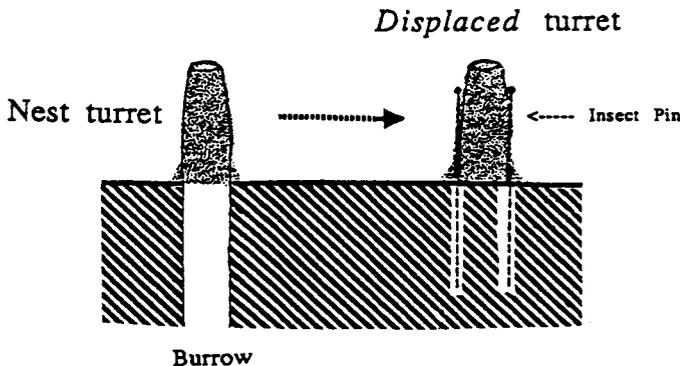


Fig. 3: Diagram showing a nest turret in situ, as well as the method for supporting the turret during manipulations

*b) Reciprocal switching of turrets:* Turrets were easily broken off intact at the base by using spatulate forceps. I placed these turrets elsewhere in the aggregation by supporting each turret on two insect pins inserted into the soil (Fig. 3). I switched the turrets from 10 pairs of nests ( $n = 20$ ) of neighboring bees (nearest neighbor distance = 1—4.2 cm,  $\bar{x} = 2.4$ ,  $SD = 1.22$ ), and for 15 additional nests I used turrets from another aggregation.

*c) Spatial displacement of turrets:* To determine if non-contact turret-derived cues are necessary for nest localization, I broke turrets ( $n = 40$ ) off at their bases and moved them  $< 30$  cm to the right or left of their original position (direction determined by a coin flip).

*d) Choice tests of own versus alien turret:* I performed choice-tests to determine if bees were able to recognize their own turret, given that other information was available. I placed a ring of 6 wooden discs around entrances ( $n = 15$  bees), and left them in place for 7 to 9 d. After this training period the visual objects and the nest turrets were displaced 1 cm to the left or right of their original positions. I covered the true nest entrance with a paste of mud made from soil collected elsewhere at the nesting site mixed with bottled, distilled water. I then pinned an alien turret into the soil 2 cm from the shifted resident turret, so that it was 1 cm to the other side of the true entrance, and recorded the responses of the returning bees.

### Experiment 3. Role of Nest Odors in Nest Recognition

*a) Cue deletions:* To determine if chemical cues emanating from the nest were important for recognition, I washed the inner wall of a 5 cm length of the burrow leading from the nest entrance (including the turret) toward the cells, using a sterile cotton swab repeatedly dipped in hexane ( $n = 30$  nests). This wash was done immediately after a female exited from her nest. These nests are referred to as "washed nests." The time between the application of hexane and the return of the bee ranged from 12 to 46 min ( $\bar{x} = 27$  min); hexane is highly volatile and presumably dissipated during this time. The same individuals were observed on all foraging trips made on the day hexane was applied. To control for possible textural changes due to swabbing, I rubbed the inner surface of the nest with a sterile cotton swab dipped in distilled water ( $n = 15$ ). To control for a simple "foul odor" avoidance effect of hexane, I applied the same volume of hexane to the outer surface of the nest entrance turret and surrounding soil ( $n = 15$ ).

I repeated the nest-tunnel hexane wash treatments on another group of bees, except that nest turrets were removed before the hexane was applied ( $n = 31$  bees). A returning bee made one approach flight, and then departed from the entrance area to begin another approach flight. I replaced the bee's unwashed turret over her entrance by resting it on two pins.

*b) Cue additions:* I collected alien female bees from nests at distant aggregations ( $> 3$  km), and placed them in groups of 10 into clean glass vials with 5 ml of hexane. I reduced this volume to 2 ml by evaporating the hexane, and stored the vials overnight in a freezer. I applied these whole-body extracts to nest entrances ( $n = 25$ ) that had been previously washed with hexane as described above.

## Results

### Orientation Behavior

Each day before their first foraging flights females engaged in brief bouts of exploratory behavior in the immediate vicinity of the nest ("orientation flights:" median duration = 7.0 s, range = 4—17,  $n = 50$ ). A female departed from her nest head first and usually walked onto the turret to face the bank. She took flight facing the nest entrance, and flew in a gradually widening serpentine pattern. After flying 1—2 m away from the bank, she flew directly towards the entrance and briefly hovered about 5 cm in front of it, with very short side-to-side oscillations. This loop was repeated two to five times, in different directions from the nest, before she flew away. In the absence of experimental manipulations or perturbations, females never made such flights on subsequent foraging trips on a given day.

### Visual Landmarks Used for Nest Localization and Recognition

Objects put in place before orientation flights did not interfere with nest localizations or recognition, nor did they induce orientation flights before subsequent same-day provisioning trips (Table 1). In contrast, objects put in place after bees made orientation flights resulted in a significantly longer elapsed "duration for entry" and greater "number of approach flights" (Table 1). Bees frequently landed on the surface of the bank, and walked over it while rapidly antennating the soil. Furthermore, before the next foraging trip bees made orientation flights of similar duration ( $\bar{x} = 7.0$  s, range = 4–15,  $n = 50$ ) to those made each day at the start of foraging activity ( $p > 0.1$ , Mann-Whitney U test).

Spatial manipulations of local landmarks did not divert the flight paths or positions of returning *L. figueresi* females, and they did not significantly alter the "duration for entry" nor the "number of approach flights." Larger landmarks such as fence posts, shrubs, trees, etc. could not be manipulated, except for preliminary trials during which a large bush was placed in front of the bank before orientation flights, which produced delays comparable to those produced by small-scale landmarks (see WCISLO 1991).

Table 1: Responses to visual objects placed near nests by *Lasioglossum figueresi* females returning from provisioning trips. Median values are given with ranges in brackets; sample sizes are given in parentheses. Within columns, values indicated by letters are significantly different from those values not sharing that letter ( $p < 0.01$ )

Experimental manipulation	Approaches to nest	Time (s) for entry into nest	Orientation flight induced?
No manipulation (49)	1 [1–2] <sup>a</sup>	6 [5–15] <sup>a</sup>	no
Cues before orientation (39)	1 [1–2] <sup>a</sup>	9 [5–20] <sup>a</sup>	no
Cues after orientation:			
1st return trip (38)	4 [2–7] <sup>b</sup>	138 [64–219] <sup>b</sup>	yes
2nd return trip (37)	1 [1–2] <sup>a</sup>	11 [5–29] <sup>c</sup>	no

### Role of Turrets for Nest Recognition

Removing turrets did not significantly increase the "duration for entry" (Table 2), nor did the spatial displacement of turrets result in any deviations in the bees' flight paths (Table 2). Manipulations involving turrets never induced orientation flights on subsequent foraging trips. During the nesting season turrets were sometimes broken off (e.g., a part of the bank erodes), and were repaired only early in the season when the soil was malleable (WCISLO et al., *subm.*). Therefore, turrets probably did not provide important visual information.

Turrets did, however, provide some olfactory or textural information. Most bees (31 of 39 females) that were searching for a nest entered it after contacting their own turret, while only one of these bees entered a foreign nest despite a total of 44 contacts with foreign turrets ( $p < 0.01$ ,  $\chi^2 = 6.78$ ). When nest entrances were covered with mud paste, and returning females given a choice between their

Table 2: Responses by *Lasioglossum figueresi* females to manipulations involving nest turrets. Other information as for Table 1

Experimental manipulation	Approaches to nest	Time (s) for entry into nest	Orientation flight induced?
No manipulation (49)	1 [1—2] <sup>a</sup>	6 [5—15] <sup>a</sup>	no
Turrets deleted (25)	1 [1—2] <sup>a</sup>	7 [5—16] <sup>a</sup>	no
Turrets shifted (40)	1 [1—2] <sup>a</sup>	9 [5—21] <sup>b</sup>	no
Neighbor turrets swapped (20)	1 [1—2] <sup>a</sup>	11 [5—19] <sup>b, c</sup>	no
Visual cues and turrets shifted (45)	1 [1—3] <sup>a</sup>	14 [5—25] <sup>c</sup>	no

turrets and alien ones, bees flew directly toward the covered entrance and briefly contacted the mud plug. They then usually hovered in front of it, flew away to begin another approach flight, or landed on the bank and walked around the vicinity of the pasted-over entrance. In these choice tests searching bees entered their turrets following antennal contact, and sometimes sat inside for up to 3 min before backing out. In contrast, bees rarely entered foreign turrets that they contacted (Fig. 4).

	MUD - PASTE COVERED ENTRANCE	
	OWN TURRET	ALIEN TURRET
CONTACTS TURRET	15	13
ENTERS TURRET	15	4

Fig. 4: Responses of female *Lasioglossum figueresi* returning to their nests for choice tests. n = 15 bees, G = 3.28, 0.1 > p > 0.05

If turrets were removed from nests and the nest tunnels were washed with hexane, the median time for one approach flight was 48 s, and no bees entered their nests (Table 3). When a bee departed for another approach flight the turret was replaced, and the median time for one approach significantly decreased (7 s), and 26 of 31 bees entered their nests (Table 3). In contrast, if other visual or chemical cues were intact, and a bee's turret was replaced with an alien one (from the same or different nesting aggregation), there were no significant effects on the bee's behavior (Table 2).

#### Role of Nest-derived Olfactory Cues

Washing the inner lining of a nest tunnel with a hexane swab significantly increased the "duration for entry" and the "number of approach flights," in comparisons with unmanipulated nests, with nests swabbed with distilled water, or with nests receiving hexane on the outer surface (Table 4). The effect induced by a hexane wash gradually decayed such that bees entered nests more rapidly on subsequent foraging trips on the same day (Table 4), and no effects were observed on subsequent days.

The application of hexane to the outside of the nest had no significant effect on the "number of approaches" nor the "duration for entry" (Table 4). The fact

Table 3: Median time for one approach flight during a return trip by a female *Lasioglossum figueresi* following the application of hexane to the inner lining of the nest tunnel; after one approach, the turret was replaced and times were recorded for subsequent approach flights, until bees entered their nests. Other information as for Table 1

Experimental manipulation	Time (s) for entry into nest	No. bees entering nest after approach
Hexane wash (31)	48 [22—82] <sup>a</sup>	0
Turret replaced:		
1st approach (31)	7 [ 5—39] <sup>b</sup>	26
2nd approach (5)	5 [ 5—15] <sup>b</sup>	4
3rd approach (1)	5	1

Table 4: Median number of approach flights and time of entry for several foraging trips on the same day following the application of hexane to the inner linings of bee tunnels; other information as for Table 1. To maintain an experiment-wise error rate of 0.05, an adjusted significance level of  $0.05/6 = 0.008$  was used

Foraging trip after hexane application	Approaches before entry	Time (s) for entry into nest
First trip (30)	5 [2—12] <sup>a</sup>	192 [70—262] <sup>a</sup>
Second trip (30)	3 [2— 5] <sup>b</sup>	112 [63—247] <sup>b</sup>
Third trip (15)	2 [1— 4] <sup>c</sup>	84 [48—128] <sup>c</sup>
Fourth trip (8)	1 [1— 2] <sup>c</sup>	33 [16— 73] <sup>d</sup>
Controls:		
Hexane on outside turret (15)	1 [1— 2] <sup>c</sup>	8 [ 5— 18] <sup>e</sup>
Distilled water (15)	1 [1] <sup>c</sup>	7 [ 5— 11] <sup>e</sup>

that bees entered a hexane-washed nest after an unwashed turret was replaced, and deposited their pollen, suggests that the bees did not avoid the odor of hexane per se, since bees still encountered that odor after they passed through the turret. The application of distilled water also had no significant effects (Table 4).

The addition of whole-body extracts of alien females resulted in a delay for the first approach flight ( $\bar{x} = 43$  s, range = 29—78). This delay was similar in duration to that produced by deleting potential cues by hexane washes ( $p > 0.1$ , Mann-Whitney U test). For the addition of cues, there was a significant correlation between "time for the first approach flight" and "total time for entry" (Spearman's  $\rho = 0.57$ ,  $p < 0.003$ ,  $n = 25$ ). Overall, however, the effect of this kind of cue addition was not as great as for cue deletions [total time for extracts:  $\bar{x} = 111$  s, range = 17—283; versus hexane washes:  $\bar{x} = 192$  s, range = 53—245 ( $p < 0.001$ , Mann-Whitney U test)].

## Discussion

### Mechanisms of Nest Recognition in Apoidea

Various studies demonstrate the importance of visual cues in nest re-location by bees and wasps (refs. in WEHNER 1981; SCHÖNE 1984; TENGÖ et al. 1990; SCHÖNE & TENGÖ 1991). *L. (D.) figueresi* females were not delayed when objects were placed in their visual fields prior to orientation flights, although the same objects altered their behavior when situated after such flights. In other Apoidea the flight paths of provisioning females can be altered by manipulating local landmarks (e.g., TURNER 1908; TINBERGEN 1972 a). In contrast, female *L. figueresi* homed directly to their nests following the displacement of local visual cues. The bees may, however, locate their nests using other visual cues (e.g., larger-scale landmarks; nest entrance patterns) which were not eliminated in this study.

Several lines of evidence suggest that *L. figueresi* females are able to use olfactory information for individual nest recognition. Following the application of a solvent to the inside of a nest, a bee entered it only after a delay, which was reduced by allowing a bee to enter her solvent-washed nest through an unwashed turret. These effects are explicable with one of several hypotheses: (1) Bees avoid the odor of hexane, and the progressive decline in "duration for entry" with each post-hexane foraging trip occurs because the hexane completely dissipates through time or the bees habituate to the foul odor; (2) the application of hexane alters visual and tactile cues used for nest recognition; or (3) bees use chemical information (produced by the bee, or strictly environmental; GAMBOA et al. 1986) to recognize their nests, and these chemical signatures are diluted by the application of hexane. The application of hexane to the outside of nests had no significant effects on bee behavior, inconsistent with hypothesis No. 1. Bees entered hexane-washed nests with un-washed turrets and unloaded their pollen, again inconsistent with this first hypothesis since they encountered any hexane odor after passing through the turret. Sexually active males of a related species are attracted to hexane extracts of females (SMITH et al. 1985), suggesting that the solvent generally dissipates with sufficient rapidity to minimize confounding effects. Such delays as described above do not unambiguously imply "disorientation," or an inability to recognize a nest. Delayed nest entry, and an increased number of looping flights, may represent evasive flight behavior (MCCORQUODALE 1986).

In choice tests, nearly all bees entered their own turret following antennal contact, yet did not enter an alien turret. Adding whole-body extracts of foreign female bees to nest entrances also significantly delayed nest entry by returning females (also HEFETZ et al. 1986; SHIMRON et al. 1985). Presumably females responded to such odors as "alien females" rather than as a "dead bee odor," which they avoided; the behavior of males to female extracts suggests there is no "dead bee" odor (e.g., SMITH et al. 1985). The protocol used in these experiments altered textural cues, but rubbing nest entrances with a cotton swab and water did not alter the behavior of *L. (D.) figueresi*, which is inconsistent with hypothesis No. 2. Nonetheless, textural cues may provide some information, since honeybees (*Apis*) on flowers can use tactile cues (KEVAN & LANE 1985).

A partial review of mechanisms of nest recognition in Apoidea is given in Table 5 (see WEHNER 1981). Individual nest recognition via chemical signatures has been proposed repeatedly, and LINSLEY (1958) even hypothesized that selec-

Table 5: Partial list of known mechanisms of nest recognition in free-living bees and hunting wasps (Apoidea); numerous taxa are known to use visual cues (see WEHNER 1981), but these have been excluded for all cases where the authors do not report information on the possible use of olfactory cues

Taxon	Visual cues?	Olfactory cues?	Glandular products in nest?	Reference
Bees (Apiformes)				
Apidae (including Anthophoridae)				
<i>Apis mellifera</i>	yes	yes	yes	FREE 1987; BUTLER et al. 1969, 1970
<i>Bombus occidentalis</i>	yes	yes	yes	FOSTER & GAMBOA 1989
<i>Xylocopa imitator</i>	yes	yes	yes	ANZENBERGER 1986
<i>X. pubescens</i>	?	yes	yes	HEFETZ et al. 1990
<i>X. virginica</i>	yes	yes?	?	RAU 1929
<i>Proxylocopa</i> sp.	yes	yes	?	BEIKO 1990
<i>Mesotrichia caffra</i>	yes	yes?	yes	SKAIFE 1952
<i>Melissodes</i> sp.	yes	yes	yes?	TURNER 1908
<i>Anthophora plagiata</i>	yes	yes	yes	STEINMANN 1985
<i>Eucera palestinae</i>	yes	yes	yes	SHIMRON et al. 1985
Megachilidae				
<i>Heriades truncorum</i>	yes	yes	yes?	STEINMANN 1976
<i>Osmia cornuta</i>	yes	yes	yes?	STEINMANN 1976
<i>O. bicornis</i>	yes	yes	yes?	STEINMANN 1976
<i>O. rufa</i>	yes	yes	?	RAW, in press
<i>Chalicodoma</i> spp.	yes	no?	yes	FABRE 1914
<i>Megachile centuncularis</i>	yes?	yes	?	RAW, in press
<i>Anthidium manicatum</i>	?	yes	?	RAW, in press
Andrenidae				
<i>Andrena vaga</i>	?	yes	yes	STEINMANN 1990
Halictidae				
<i>Lasioglossum</i> ( <i>D.</i> ) <i>zephyrum</i>	yes	yes	yes	KUKUK et al. 1977
<i>L. (D.) figueresi</i>	yes	yes?	yes	Results
<i>L. (E.) malachurum</i>	?	yes	yes	AYASSE 1990
Hunting wasps (Spheciformes)				
<i>Ammophila campestris</i>	yes	no	no	BAERENDS 1941
<i>Bembix</i> spp.	yes	no	no	VAN IERSEL 1975;
		(yes?)		NIELSON 1945
<i>Philanthus triangulum</i>	yes	no	no	TINBERGEN 1972 a
<i>Cerceris</i> spp.	yes	no?	no	TSUNEKI 1965
<i>Sceliphron caementarium</i>	yes	no	no?	FERGUSON & HUNT 1989
<i>Psenulus fuscipennis</i>	yes	yes	yes	STEINMANN 1976

tion for such abilities would be more pronounced in populations nesting in large aggregations (also HEFETZ & GRAUR 1988). For some bees individual chemical profiles at nest entrances result from Dufour's gland secretions (HEFETZ 1987), but bioassays either need to be made to determine any function (e.g., BROOKS & CANE 1984), or they did not demonstrate a recognition function (HEFETZ et al. 1982). In other cases bioassays demonstrated individual recognition abilities, but chemical analyses are lacking (e.g., Results; STEINMANN 1973, 1985, 1990).

In some Apoidea nest recognition may be equivalent to nest localization ("topographic nest recognition"). FABRE (1914) switched mud nests between pairs of mason bees (Megachilidae), and bees continued to work on the alien nests at the familiar localities. BAERENDS (1941) also manipulated nests, and concluded that olfactory nest attractants were not necessary for nest recognition in *Ammophila*. EVANS (1966) reviewed earlier studies, and found no convincing evidence that olfactory cues are used by wasps for nest recognition. CHMURZYŃSKI (1964) also reviewed earlier studies, but believed that nests are distinguished from others by smell or touch. TINBERGEN (1972a: p. 117) showed that *Philanthus* females perceived pine odors near nest entrances, but did not use them as nest recognition cues, and he concluded that there is no evidence for olfactory cues originating at the nest. STEINMANN (1976) showed that a *Psenulus* (Pempredonidae) wasp has nest entrances with individually distinctive odors. PFENNIG & REEVE (1989) cite studies in preparation on a *Sphecius* wasp that "can discriminate between soil collected from the entrance of a neighbor's burrow and soil collected from a nonneighbor's burrow (p. 16)". To date there is little supporting evidence for olfactory nest recognition in Spheciformes, in contrast to bees (Table 5), although the scanty evidence highlights the need for further studies.

Studies specifically addressing the role of olfactory cues for nest recognition in Spheciformes will be interesting because they use such cues in contexts such as hunting prey (TINBERGEN 1972b; STEINER 1983; GNATZY et al. 1990) or mating (EVANS & O'NEILL 1988); they have well-developed glands in at least some species (HEFETZ & BATRA 1979; DUFFIELD et al. 1981); their antennae have numerous olfactory receptors (ÅGREN 1989); and some parasites are attracted to wasp nests in part by olfaction (WCISLO 1986; ROSENHEIM 1987). Furthermore, these wasps are remarkable in their ability to return home even after the nesting site has been totally trampled underfoot, and nest entrances buried with soil. In various species these "lost" wasps frequently touch the soil with the tips of their antennae (pers. obs.). Landmarks on the horizon are usually available in such cases, however, and these can provide information for orientation (VAN IERSEL 1975).

### Recognition, Contextual Changes, and Social Evolution

HÖLLDOBLER & MICHENER (1980) and others suggested that possible contexts for the evolution of kin recognizing abilities in solitary species include mate recognition (e.g., WCISLO 1987, 1992) and nest recognition. Such evolutionary transfer of signal usage from one context to another is widespread (refs. in OTTE 1974; WEST-EBERHARD 1984; HÖLLDOBLER & CARLIN 1987). The relevant context

for understanding social evolution obviously involves behavior at the nest. Other factors such as olfactory recognition and learning abilities predate the evolution of the Aculeata, occurring also in other Apocrita (e.g., PAPAJ & VET 1990).

Numerous bee lineages use glandular secretions in nest architecture (MICHENER 1969), especially to line brood cells or nest entrances. In contrast, such secretions apparently are rare in spheciforme wasps, and I know of published reports only for Pemphredonidae (e.g., MALYSHEV 1968). A mason bee adds glandular secretions to its nest, possibly to render it hydrophobic (KRONENBERG & HEFETZ 1984), and mud-daubing wasps may do the same (BROCKMANN, in litt.). Further studies on Spheciformes are needed to substantiate 1) any differential use of glandular material in nest architecture within Apoidea, and 2) the use of this material as sources of olfactory information in nest recognition. The use of metabolic products in nest construction leaves chemical profiles in nests. Since offspring emerge into this environment, they may learn and/or acquire these odors, potentially facilitating kin-based social evolution (cf. HÖLLDOBLER & MICHENER 1980; MICHENER 1982). Nest odors are known in various eusocial Hymenoptera (e.g., VERLAINE 1925; KUKUK et al. 1977; GAMBOA et al. 1986; FERGUSON et al. 1987; HÖLLDOBLER & WILSON 1990), which are sometimes associated with kin recognition cues (BREED et al. 1989; ESPELIE et al. 1990; GAMBOA et al. 1986). The exceptional eusocial sphecids are also pemphredonids (MATTHEWS 1968; ROSS & MATTHEWS 1989; also MATTHEWS & NAUMANN 1988; MCCORQUODALE & NAUMANN 1988); this is the only spheciforme family for which there is positive evidence for olfactory nest recognition (Table 5).

Comparative information from other animals is inconclusive with respect to the above hypothesis. The only known social isopods use pellets of feces (metabolic wastes) to line their nest entrances. This lining is used for nest recognition, and similar chemical badges may be used to discriminate among kin (LINSINMAIR 1987; HOFFMANN 1985). Subsocial female earwigs (Dermaptera) deposit individual-specific recognition pheromones on their brood chambers (RADL & LINSINMAIR 1991). Some dung beetles (Scarabaeinae) have elaborate brood care, yet there are no known eusocial species, and brood parasitism is rare (HALFFTER & EDMONDS 1982). In scarabaeine lineages such as *Copris* the female produces a black secretion which hardens as a smooth internal surface of the brood chamber. Other lineages lack such obvious coatings, but HALFFTER & EDMONDS (1982) believe that females of nearly all species apply secretions with antibiotic properties.

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