

William T. Wcislo · Bertrand Schatz

Predator recognition and evasive behavior by sweat bees, *Lasioglossum umbripenne* (Hymenoptera: Halictidae), in response to predation by ants, *Ectatomma ruidum* (Hymenoptera: Formicidae)

Received: 7 August 2002 / Revised: 8 November 2002 / Accepted: 12 November 2002 / Published online: 19 December 2002
© Springer-Verlag 2002

Abstract *Ectatomma ruidum* is an abundant soil-nesting Neotropical ant, which displays extensive behavioral flexibility during foraging activities. We studied here one unusual element of their behavioral repertoire: ambush predation. A worker of *E. ruidum* waits near a nest of a social sweat bee, *Lasioglossum umbripenne*, lunging at incoming bees, or less frequently, at departing bees. However, bees detected ambushing ants and modified their behavior. Dead ants placed at bees' nest entrances significantly decreased bee activity, indicating that bees recognized dead ants as potential predators. Neither simple black models (square and rectangle) nor olfactory cues had any effect on overall bee activity. A returning bee usually approached her entrance and immediately entered, but if an ant was waiting at the nest, a bee was significantly more likely to abort the first approach flight and then to re-approach the nest on the side opposite the ant's position. As models became increasingly ant-like, returning bees more frequently aborted their first approach flight, expressing other behaviors before entering nests. These behaviors included withdrawal followed by an approach from a different direction; zigzagging flights, either from a distance or close to the entrance or even a close inspection; landing a short distance from the nest, then approaching on foot or waiting for several seconds before entering. Ants responded with effective counter-behaviors. Behavioral flexibility in nest entering/exiting by *L. umbripenne* and in hunting strategy by *E. ruidum* shows the complexity of this predator-prey re-

lationship, and illustrates the importance of information processing by both species involved in determining the outcome of the interspecific interaction.

Keywords Behavioral flexibility · Anti-predator behavior · Pattern recognition · Predator-prey relationships

Introduction

Foraging animals strike a balance between attention to resource acquisition and predation risk (reviewed in Bernays and Wcislo 1994; Helfman and Winkelman 1997). Predation risk represents a cost, which foragers can reduce via an assessment mechanism that enables predator recognition, followed by appropriate defensive or evasive action. Predator recognition is well known in vertebrates (Hinde 1954; Tinbergen 1960; Curio 1976; Cheney and Seyfarth 1990; McLean and Rhodes 1991; Gill and Sealy 1996; Clutton-Brock et al. 1999). In contrast, predator recognition has been little studied in insects and other invertebrates (Curio 1976; Chivers et al. 1996; Jackson and Pollard 1996; Wisenden et al. 1997), and some studies failed to detect any predator-recognition mechanisms. Neither introduced honey bees (*Apis*) nor native bumble bees (*Bombus*), for example, show any evasive behavior with respect to predatory crab spiders (Thomisidae) which are "sit-and-wait" predators on flowers and major enemies of the bees (Morse 1986; Cartar and Dill 1991). In other cases, evasive behavior has been found, not only in situations of predator avoidance, but also when females avoid conspecific males (Batra 1965; McCorquodale 1986; Stone 1995).

Ants are among the world's premiere predators, and the most important predators of other social insects, especially in the tropics; ponerines are among the most predatory ants (Jeanne 1979; Hölldobler and Wilson 1990). Throughout their long history, ants have evolved diverse predatory strategies, to which other social insects have responded with various defensive strategies

Communicated by R.F.A. Moritz

W. T. Wcislo
Smithsonian Tropical Research Institute, Apartado 2072, Balboa,
Ancón, Republic of Panamá

B. Schatz (✉)
Centre d'Ecologie Fonctionnelle et Evolutive (CEFE),
CNRS-UPR 9056, 1919 route de Mende,
34293 Montpellier Cedex, France
e-mail: bertrand.schatz@cefe.cnrs-mop.fr
Fax: +33-4-67412138

(Hölldobler and Wilson 1990). In response to ant predation, some social insects flee and abandon the nest, while others fight the ants, or use physical and chemical barriers to protect the nest (e.g., Skutch 1971; Michener 1974; Jeanne 1975; West-Eberhard 1989; Wenzel and Pickering 1991; Kojima 1993). Well-known anti-predator behaviors effective against ants include the projection of repellent substances, the employment of specialized defensive behaviors, and even suspension from a rapidly excreted silk strand by which some caterpillars isolate themselves from ants (Maschwitz et al. 1981; Hölldobler and Wilson 1990; Freitas and Oliveira 1996; Dejean et al. 2001; Di Giusto et al. 2001).

This paper documents another means of avoiding ant predation. Female sweat bees, *Lasioglossum (Dialictus) umbripenne* (Hymenoptera: Halictidae), take evasive action to avoid attempted ambush by an ant, *Ectatomma ruidum* R. (Hymenoptera: Formicidae, Ponerinae). For the ants, behaviors that increase the efficiency of predation will be favored, because bees are a significant protein source, and exploiting this source increases colony size (Schatz and Wcislo 1999). For the bee, any behavior that diminishes the intensity of ant predation will be potentially beneficial because a colony will maintain a larger number of foragers gathering more food per unit time. However, predation also imposes an indirect cost, because behaviors necessary to avoid it should decrease foraging efficiency. We conducted observations to determine whether the ambushing ants could impose a delayed nest-entering or nest-exiting of bees, which could decrease their foraging activity. We then conducted observations and experiments to determine whether bees recognize ambushing ants solely on the basis of visual cues, or if olfactory cues are also important. We also examined the extent to which bees modify approach flights, and overall activity, depending on whether or not an ambushing ant is present. The description of evasive behavior of bees and counter-moves by ants led us to a better understanding of how behavioral flexibility shapes this predator-prey interaction.

Methods

Study sites

Observations and experiments were conducted in March/June 1997, and 1–15 April 1998, at a nesting aggregation of *L. (D.) umbripenne*. The study site is in east-central Panamá Province, Republic of Panamá (9°18'02"N, 78°57'31"W), 7.5 km north from the Pan-American Highway, along an unpaved road running from El Llano to Cartí (Schatz and Wcislo 1999).

Sweat bees

L. (D.) umbripenne females are small bees (body-length= \sim 4–5 mm) that nest in the soil, with 1 to approximately 80 females per nest (median=7); they occur widely throughout the Neotropics and locally can be very abundant (Wille and Orozco 1970; Eickwort and Eickwort 1971; Wcislo 1989, 1997). Nests are usually in aggregations that can have >1,500 nests in an approximate-

ly 10x50 m area (mean nest density=3.5 nests/m²; maximum nest density=32 nests/m²; Schatz and Wcislo 1999). Nests isolated by hundreds of meters from all others occur but are rare. Nest aggregations often occur in open, cleared areas along the edges of roads and trails. Within aggregations, bees nest in spatial proximity to one another and the nest entrances can be separated by as little as approximately 2 mm. The interactions that we describe occur in the immediate vicinity of a bee nest, on accumulated soil tailings ("tumulus") that surround an entrance. The tumulus can be blown or washed away, leaving behind a "chimney" several millimeters tall, or the entrance can be nearly flush with the soil surface.

Bees begin foraging between 0800 and 0900 hours, and make repeated foraging trips per day (W.T. Wcislo, unpublished data). A returning bee typically flies straight to the nest entrance (hereafter, an "approach") and enters. However, if a returning bee perceives a disturbance in its visual field (e.g., a major change in the constellation of local landmarks; Wcislo 1992; Zeil et al. 1996), then it aborts the approach and flies away from the entrance to approach again. It repeats these approach-withdraw sequences a number of times before entering the nest. On occasion, especially if there are strong winds, bees land near (< approximately 1 cm) the entrance and walk inside. Nests with multiple females have a guard stationed just inside the entrance which excludes unfamiliar bees (non-nestmates). Each returning female waits briefly while the guard assesses the forager's identity, and this brief pause creates an opportunity for the ant to pounce on its prey.

Ants

E. ruidum is a medium-sized (body length, 8–9 mm), soil-nesting ant, which is abundant throughout the Neotropics in natural and disturbed habitats (Schatz and Wcislo 1999 and references cited therein). Mature colonies usually have 70–100 ants, but larger colonies (>200 ants) are known. Foraging within a small home range (<3 m from the nest), workers are generally solitary hunters even though they may display a finely graded recruitment linked to prey mass (Schatz et al. 1997). This species is an efficient predator because workers express a diverse array of learned foraging specializations (Schatz et al. 1996, 1999; Schatz and Wcislo 1999). At some localities, *E. ruidum* foraging workers adopt a sit-and-wait mode of predation at *L. umbripenne* nest entrances, and a single ant colony collects a mean of 25 bees per day during the middle dry season when bees are most abundant (Schatz and Wcislo 1999). Due to the fact that both *Lasioglossum* and *Ectatomma* are central place foragers, the ants exact a heavy toll from the same bee nests, and potential prey repeatedly encounter the same predators. An ambushing ant waits at a bee-nest entrance, and lunges at bees returning with pollen, or those exiting the nest (for details, see Schatz and Wcislo 1999). If successful, the ant stings the bee and carries it home; if not, she usually continues hunting at the same nest or a different one. Occasionally, ants try to grab a guard or force their way past one, but they are blocked by the small entrance diameter of the bee nest, and the guard often turns around 180° to block the entrance with its metasomal tergites.

Methods

For naturally foraging females returning to undisturbed nests, we recorded whether a bee entered the nest following a first approach flight, and whether an ant was present. We counted, for a 5-min period, the number of bees entering and exiting a nest. Foraging activity was sampled only once for each nest.

One set of experiments determined whether bee-activity levels were modified when ambushing ants were present. Operationally, we defined "activity level" as the sum of entrances plus exits per time period. We experimentally presented one of four different stimuli at a nest entrance: (1) Dead ant: individual *E. ruidum* ants were collected and killed by freezing. The ant's alitrunk was pierced with a no. 1 insect pin, and the ant was placed at the nest entrance, with the head facing the entrance at a distance of ap-

proximately 1 mm. The ant's tarsi just touched the soil surface so that the body was about 2 mm above the soil surface. (2) Black rectangle: a black rectangle in cardboard approximately the same size as the ant (1.8×6.6 mm) was pinned and presented at the nest entrance as described for the dead ant, approximately 2 mm above the soil surface. (3) Black square: a black square (also in cardboard) with the same area as the rectangle was pinned and presented at the nest entrance as described for the rectangle. (4) No stimulus: this treatment documented the behavior of the bees in the absence of any manipulation; we included only those bees that returned when there were no ants naturally present. A model was presented at a nest in a randomized order, either north, south, east, or west of the entrance, with the direction randomized. We left the model in place for a 5-min period and counted the number of bees entering and exiting a nest. The number of bees was sampled only once for each nest.

To determine whether bees responded to visual or olfactory cues, two trials were done, using recently killed ants and frozen ones. In the first trial, ants were captured, killed by freezing, and allowed to air dry before being presented to bees at the nest entrances; they were divided into two groups. One group was washed with hexane to remove cuticular hydrocarbons and other compounds, while the other group was unwashed. In the second trial, ants were captured in the field, killed by freezing, and divided into two groups; one group was washed with hexane and the other group was unwashed. Both groups of the second trial were kept frozen until they were presented to bees, generally corresponding to a period of 24 or 48 h, while both groups of the first trial were killed by freezing (less than 5 mins), and were kept to air dry before being presented to bees. Washed and unwashed ants were presented separately at nest entrances as described above.

Another set of experiments provided more detailed data on the bees' responses to the models. We used the same models as be-

fore, and also opportunistically scored bees' behavior when a living ant was naturally hunting. During these presentations we used specific categories to describe the behavior of returning bees, as follows: (1) Direct entry: a female entered the nest without hesitation (as before); (2) Approach-withdraw: a female approached the nest directly but then withdrew from the immediate area beyond our field of view; (3) Distant zigzag: a female flew 10–50 cm above the nest in a serpentine (zigzag) pattern; (4) Local zigzag: a female flew in a serpentine pattern within 10 cm of the nest; (5) Close inspection: a female flew at the model, and briefly contacted it; (6) Land and walk: a female landed within 1–2 cm of the nest tumulus and immediately entered by walking; (7) Land and wait: a female landed within 1–2 cm of the nest and waited 5–15 s before entering.

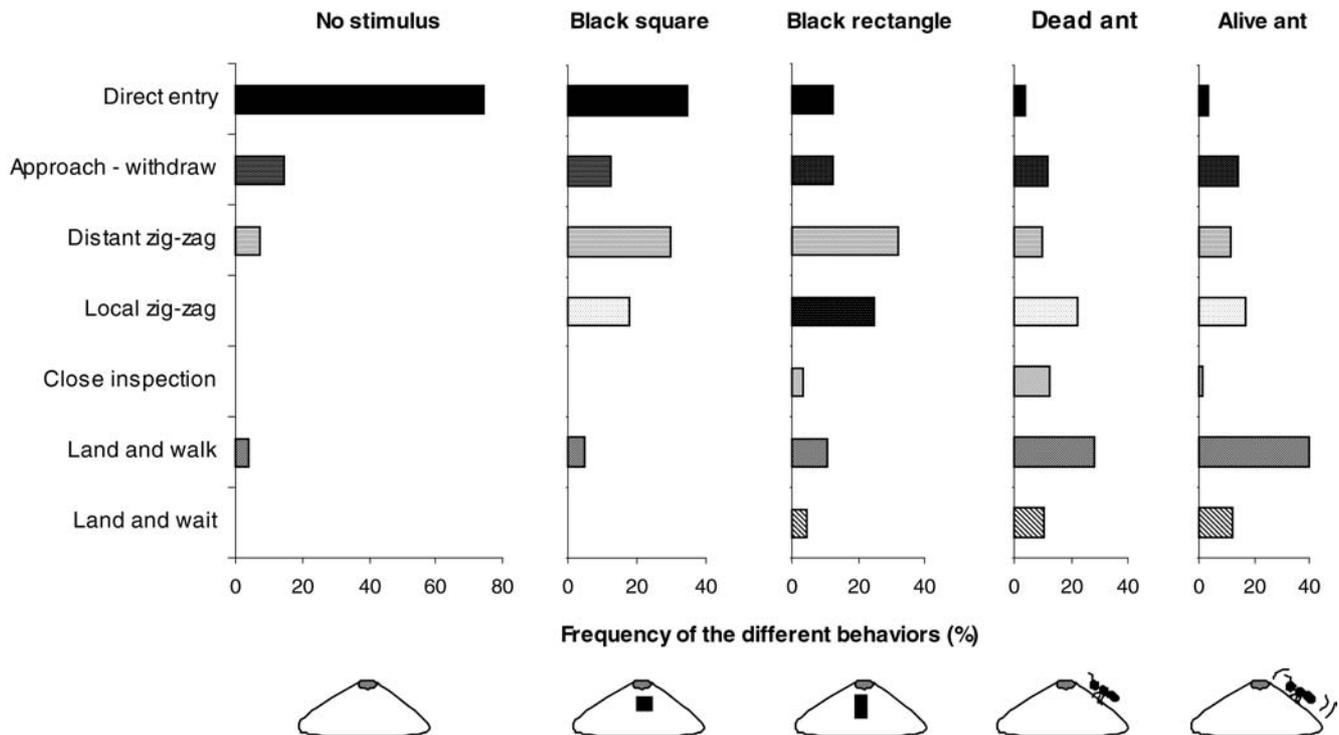
We also estimated the compass direction of bees returning to the nest when an ant was present. We used the ant's position as a 0° mark, which allowed us to divide the compass into 45° sectors, and then to visually estimate in which sectors the bees landed. These approach angles were compared with those for bees returning to nests where no ants were present. Data with circular distributions were analyzed using Oriana v1.05 (Kovach 1994), and the other data were analyzed using SYSTAT v7.0. Voucher specimens of the bees and the ants are in the Dry Reference Collection of the Smithsonian Tropical Research Institute (Panamá), and the Cornell University Insect Collection (Ithaca, New York).

Results

Behavior under natural conditions

A returning forager usually approached a nest and entered it directly if no ants lurked nearby, and only 14.5% (18 of 124 returning bees: cases of "no stimulus" on Fig. 1) aborted the first approach flight. In contrast, when an ant was waiting at a nest, most of the bees (116 of 120 returning bees, 96.7%: cases of a live ant in Fig. 1) aborted the first approach flight at a significantly higher frequency than when no ant was present

Fig. 1 Behavioral responses of female *Lasioglossum umbripenne* bees: under natural conditions with no ant present (*no stimulus*) ($n=124$), or when they encounter a *black square* ($n=118$), a *black rectangle* ($n=130$), a dead, pinned *Ectatomma ruidum* ant ($n=120$), or a live *E. ruidum* ant ($n=120$). See text for definitions of the behavioral responses



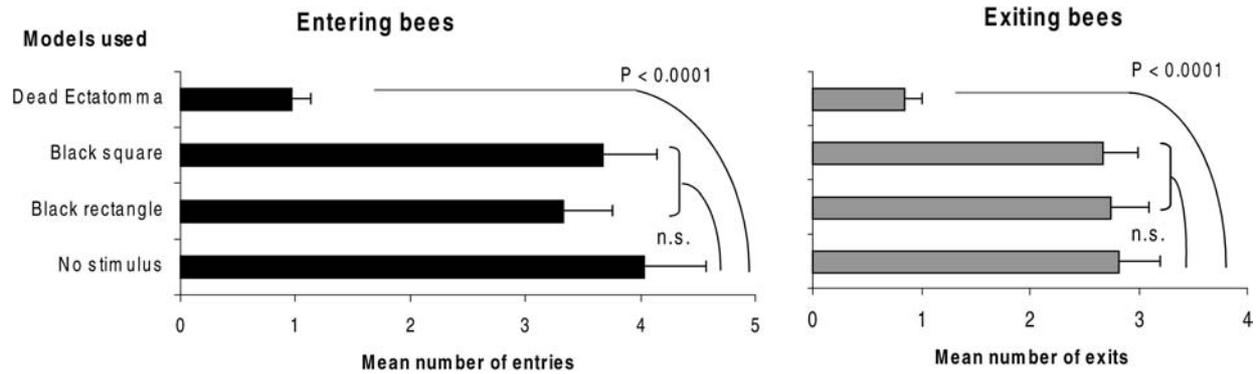


Fig. 2 Number of female *LasioGLOSSUM* entering and exiting nests per 5-min periods when different models were present at nest entrances ($n=49$ for each model). Means are given \pm standard errors; see text for comments and statistical analysis

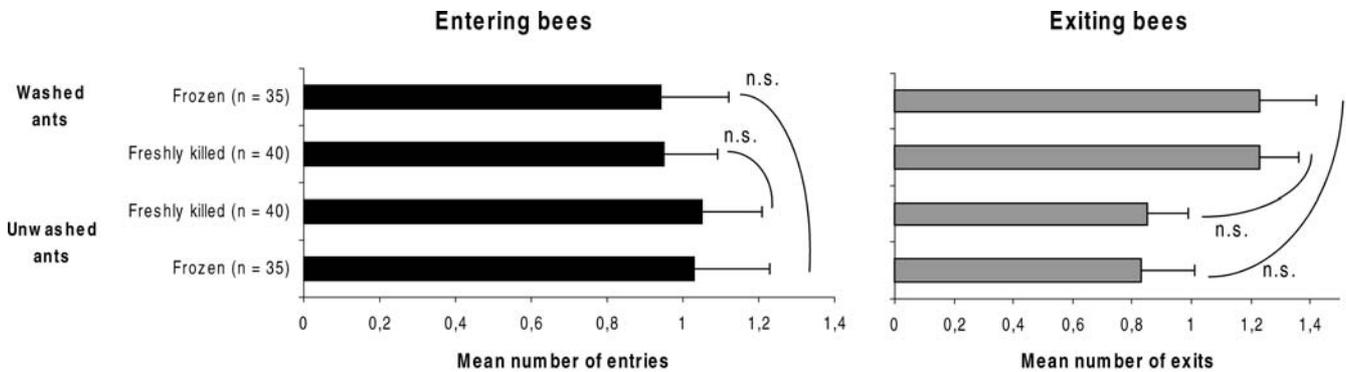


Fig. 3 Number of female *LasioGLOSSUM* entering and exiting nests per 5-min periods in response to frozen, dead ants versus dead ants that had been washed in solvents. Means given \pm standard errors; see text for comments and statistical analysis

(Pearson's $\chi^2=166.2$, $P < 0.0001$). Following the aborted approach, bee behavior varied. In general, the bees displayed distant zigzag (14 of 116 flights), or local zigzag (20 of 116 flights), or even some close inspections (2 of 116 flights). Bees flew around the nest to the other side and approached the ant from behind (63 of 116 flights). In most of these latter cases, the ant successfully tracked the bee (42 of 63 cases, 66.7%), as indicated by changes in the ant's body position, and sometimes reached to capture a bee (12 of 42 cases, 28.6%), entering by walking. An ant waiting at a nest was sometimes distracted by a different bee returning to a neighboring nest. As the other bee flew into the ant's visual field, the ant turned to track it, and the first bee immediately flew toward the nest and entered.

Evasive behavior of bees in response to manipulations

Detection of ambushing ants by bees

The experimental treatments significantly decreased the number of bees entering and leaving nests (Fig. 2; entering bees: Kruskal-Wallis test statistic=35.87, $P < 0.0001$,

assuming a χ^2 distribution with $df=3$; exiting bees: Kruskal-Wallis test statistic=30.25, $P < 0.0001$, assuming a χ^2 distribution with $df=3$). Repeated Mann-Whitney U -tests using a Bonferroni adjusted alpha level ($\alpha=0.0083$) showed that there were no significant differences in activity level between the control (no model presented) and either the black square ($P > 0.7$ for both entering and exiting bees) or black rectangle ($P > 0.7$ for both entering and exiting bees). Likewise, there was no significant difference in activity in the presence of a black square or black rectangle (Mann-Whitney $U=1176$, $P > 0.8$ for both entering and exiting bees). In contrast, there was a significant difference in bee activity between the control and the dead ant (entering bees: Mann-Whitney $U=1904$, $P < 0.0001$, Pearson's $\chi^2=26.11$ with $df=1$; exiting bees: Mann-Whitney $U=1803$, $P < 0.0001$, Pearson's $\chi^2=19.7$ with $df=1$). These results indicate that bees can distinguish between ants and models using either visual or chemical cues and use this information to modify their nest-entering behavior.

The median number of bees entering or exiting nests per 5-min period did not differ between washed and unwashed ants, regardless of whether frozen or freshly killed ants were presented to bees. Comparison of washed and unwashed ants gave the following results (for frozen ants: bees entering, Mann-Whitney $U=622$, $P=0.91$; bees exiting, Mann-Whitney $U=487$, $P=0.12$; for freshly killed ants: bees entering, Mann-Whitney $U=831$, $P=0.75$; bees exiting, Mann-Whitney $U=639.5$, $P=0.15$; Fig. 3). These

findings show that bees responded to visual cues, and not olfactory or contact chemical cues.

Subsequent graded response behavior of returning bees

Models presented at nest entrances significantly changed the frequencies of different bee behaviors, relative to those returning to unmanipulated nests (Fig. 1: Kruskal-Wallis=247.3, $P < 0.0001$ assuming a χ^2 distribution with $df=4$). The frequencies of different bee behaviors were significantly different when bees were confronted with a black square versus a black rectangle ($P < 0.001$, Pearson's $\chi^2=26.61$ with $df=6$), while they were slightly different when bees were confronted with a dead ant versus a live ant ($P < 0.05$, Pearson's $\chi^2=14.07$ with $df=6$). As the ant model became increasingly life-like, bees were more likely to modify their flight behaviors, which cumulatively accounts for the differences in overall activity levels (Fig. 1). The fact that presence of a black rectangle or square did not modify activity levels, but that presence of a dead ant did (Fig. 1), indicates that bees responded to the ant as a potential threat, and not that they were lost and confused by the presence of an object or landmark that differed from those the bees had learned for nest localization.

In response to models, bees frequently approached them from varying directions, by either approaching a nest and then withdrawing, or by flying in a zig-zag pattern at varying distances from the nest (Fig. 1). The frequency of the "approach and withdraw" response was nearly constant (approximately 0.13) for the different models. Such approach flights could help the bee better resolve the image (see Land 1997), or they might distract the ant (as described above) when a waiting ant shifts attention to a bee returning to a neighboring nest. When bees encountered living or dead ants, they most frequently landed near the nest and then entered by walking. The proportion of bees that landed was greater when bees encountered living versus dead ants, but the difference was not significant (Mann Whitney U -test, $P > 0.05$). There was also a notable decrease in the frequency of bees contacting a living ant ("close inspection") in comparison with a dead ant ($P < 0.0001$, Pearson's $\chi^2=24.08$ with $df=1$), indicating that bees also make use of information about movement, if available.

When no ants were present, the distribution of compass directions for returning bees did not differ significantly from a uniform distribution (Rayleigh test of uniformity=0.6, $n=74$). In contrast, when ants were present, the compass directions of returning bees were significantly clumped (Rayleigh's test of uniformity=0, $P < 0.05$, $n=64$), with a mean vector opposite the position of the ant ($181.9 \pm 4.5^\circ$). Mean vectors of angles for bees returning to nests with and without waiting ants were significantly different (no ant waiting, $132.6 \pm 55.3^\circ$, Watson's F -test for circular means=4.2, $P < 0.01$). These data show that bees can perceive ambushing predators and land in a more distant sector to avoid the predator.

Responses of ants to evasive behavior of bees

In response to the zigzagging approach of the bee, particularly local zigzag (Fig. 1), ants often rapidly and excitedly pirouetted atop the nest entrance, apparently surveying the 360° area surrounding the nest, which helped facilitate the capture of bees that landed some distance from the nest entrance and walked in on foot. This counter-behavior was associated with approximately 18% of the 76 successful prey captures studied by Schatz and Wcislo (1999), and is an effective counter-measure to capture bees that enter their nests in the unusual manner of walking.

Discussion

The results confirmed that bees perceive ants as a potential threat or risk (Schatz and Wcislo 1999), and modify their behavior to avoid them. The avoidance behavior was mainly based on visual pattern recognition of an *E. ruidum* worker. The use of models showed that bees gradually adopted a more prudent nest-approaching behavior (increasing proportion of "zigzag" flights, "land and walk", and "land or wait", and decreasing proportion of direct entries) as the ant model became increasingly life-like. It could be postulated that the geometrically shaped models, particularly the square, were perceived by bees as unfamiliar landmarks that disturbed the visual recognition of the nest entrance. However, our results show that both these shapes were treated as objects confusable with an *E. ruidum* worker, and induced significant changes in the nest-approaching behavior of bees. Nevertheless, the two black shapes did not change overall activity levels (entries or exits), suggesting that the delay induced by the change of the behaviors displayed did not incur a significant time loss. Ant recognition was also influenced by ant movements, because the bees' behavior was also modified depending on whether a living or a freshly killed ant was present at the nest entrance. It is unlikely that the multiple approach flights or altered directions observed in response to presence of ant-like objects function to better resolve the image (Land 1997), although the behavior may have that effect. This hypothesis predicts that bees respond similarly to the different models, which we did not observe. In response to a threatening stimulus, bees sometimes responded by flying directly at the ant, exhibiting behavior similar to that of other *Lasioglossum* bees toward parasitic velvet ants (Hymenoptera: Mutillidae) (Batra 1965), analogous to the predator-mobbing behavior of birds (McLean and Rhodes 1991). More frequently, however, bees tried to avoid the ants: they made repeated approach flights, altered flight directions, or changed approach styles (walking vs flying). Such graded responses illustrate that potential prey respond in a manner that reflects the magnitude of the threat posed by a predator (reviewed in Helfman and Winkelman 1997).

Furthermore, a comparison between ants that were washed versus unwashed in a solvent (and therefore putatively with and without cuticular hydrocarbons) showed no significant differences in the bees' behavior, indicating that they use vision rather than olfaction to recognize ants. Stingless bees (*Trigona*) also use vision to detect and avoid spider webs (Craig 1994a, 1994b). Other invertebrates, such as damselfly larvae (*Enallagma*, Odonata), recognize predators using learned chemical cues (Chivers et al. 1996; Wisenden et al. 1997). Mayfly nymphs (*Baetis*, Ephemeroptera), in contrast, change their behavior by seeking refuge when exposed to a live fish, but chemical cues derived from fish (a minnow, *Phoxinus*) or chemical cues plus a fish model did not significantly increase refuge-seeking behavior (Tikkanen et al. 1996). If the entering bees visually detected ambushing ants, the next logical question is, how do bees inside the nest acquire information about ant presence? The existence of a tunnel several centimetres long between the entrance and the first chambers, which allows passage of a single bee (Wille and Orozco 1970; Wcislo 1989, 1997), delays the contact between entering and exiting bees, rendering difficult or impossible the exchange of relevant information about ant presence. As a consequence, to get information about ant presence, bees planning to exit would be expected to come out, inspect the nest entrance and quickly back down again into the entrance if an ant is present. This behaviour is certainly associated with a significant number of captures by ambushing ants on exiting bees, and could explain why some bees were seized head-first (Schatz and Wcislo, 1999).

The ambush strategy used by *Ectatomma* to attack bees is apparently not common in this genus (see Schatz and Wcislo 1999), despite the fact that *Ectatomma* spp. are frequently very abundant (e.g., Levings and Franks 1982; Schatz et al. 1997 and references cited therein), and are often found in areas where ground-nesting bees and wasps of an acceptable size occur in abundance (W.T. Wcislo, unpublished data). Moreover, the localization of *L. umbripennis* nest aggregations changes from year to year, relative to the ant nests. Consequently, it is unlikely that bees have an automatic response to this predator, although this study did not address the ontogeny of recognition and evasive behavior. It would be interesting to know which ant features are used by bees in predator recognition. Among vertebrates, predator and prey detection is brought about by selective attention to specific phenotypic features (Langley 1996), and naive individuals can learn to recognize a predator after one-event learning (Maloney and McLean 1995). We also do not know the ontogeny of the ants' ambushing behavior, but it too is likely to be learned, as are many foraging strategies of *Ectatomma* (Schatz and Wcislo 1999; Schatz et al. 1999). Preliminary evidence indicates that ants are more likely to take up an ambushing position at more populous nests, where bees are coming and going more frequently, than at nests with few or solitary bees (W.T. Wcislo, unpublished data). However, bees nesting

in areas of an aggregation with high densities might passively avoid predation, because ambushing ants are distracted by other bees returning to neighboring, non-target nests. Therefore, gregarious nesting may provide "selfish herd" benefits (Hamilton 1971; Wcislo 1984; Rosenheim 1990).

Evasive behavior – unpredictable changes in an erratic flight path in response to a threat – has been described in different contexts for other aculeate Hymenoptera (bees, wasps, ants). For example, females of the solitary bee, *Anthophora plumipes* (Apidae), become sexually unreceptive after mating, yet males continue to attempt copulation with unreceptive, foraging females (Stone 1995). When males repeatedly harass a female, she responds by changing her flight path and flies rapidly at a low altitude among the bushy herbs (*Symphytum orientale*) on which she forages, and males lose visual contact (Stone 1995). Evasive behavior has also been described for two digger wasps (*Crabro argusinus* and *Philanthus inversus*, Sphecidae) (McCorquodale 1986). Females of these ground-nesting wasps are attacked by brood parasitic "satellite" flies (*Senotainia*, Sarcophagidae; Miltogramminae) as the wasps return to their nests with prey. The flies pursue the wasps, precisely tracking their flight paths, and when in target range the flies flick first-instar larvae at the wasps' prey. When pursued by satellite flies, these wasps engage in erratic flight, increasing the number and frequency of turns. Here, an ability to identify and evade predators is beneficial for the bees up to the point at which evasive behavior renders foraging too inefficient (Clark and Dukas 1994). We hypothesize that a decrease in activity (exits+entrances) also decreases the quantity of pollen and nectar that is brought into the nest per unit time. Differential predation or threats of predation could constitute a potential explanation of the reduced individual efficiency in larger colonies of social halictid bees and other social insects than in smaller ones, even if the potential existence of similar differential parasitism should also be considered (Michener 1974; Wenzel and Pickering 1991). The bees evade the ants in various ways, but one of the common ways is to approach the nest in an unusual manner, on foot. In response, the ants displayed a second attack behavior (pirouette behavior) that enabled them to capture additional prey. Such a behavior suggests that the ant was able to detect bees displaying zigzag flight above the nest entrance. This ability of *E. ruidum* workers is not surprising when one considers that its number of ommatidia is relatively high among ants (Gronenberg and Hölldobler 1999). Flexibility in nest entering-exiting behavior of *L. umbripennis*, in the face of flexible hunting strategies by *E. ruidum* (Schatz et al. 1996, 1997; Schatz and Wcislo 1999), illustrates the dynamics of a complex predator-prey relationship, and the importance of information processing by the species involved in determining the outcome of an interspecific interaction (Bernays and Wcislo 1994; Schatz et al. 1997).

Acknowledgements We thank Hermógenes Fernandez for help with field work, Cole Gilbert, Jochen Zeil, and Eric Warrant for answering questions about insect vision, and Nico Franz and Laura Arneson for helpful criticisms on the manuscript. We also thank Doyle McKey for improving the English text. This work was supported by general research funds of the Smithsonian Tropical Research Institute to W.T.W., and by an STRI Short-term Fellowship to B.S. We are also grateful to the Autoridad Nacional del Ambiente of the Republic of Panamá for permits to work in the field. The work presented in this paper was conducted in full compliance with all current laws of the Republic of Panamá.

References

- Batra SWT (1965) Organisms associated with *Lasioglossum zephyrum* (Hymenoptera: Halictidae). *J Kans Entomol Soc* 38: 367–389
- Bernays EA, Wcislo WT (1994) Sensory capabilities, information processing, and resource specialization. *Q Rev Biol* 69: 187–204
- Cartar RV, Dill LM (1991) Costs of energy shortfall for bumble bee colonies: predation, social parasitism, and brood development. *Can Entomol* 123:283–293
- Cheney DL, Seyfarth RM (1990) How monkeys see the world. University of Chicago Press, Chicago
- Chivers DP, Wisenden BD, Smith RJF (1996) Damsel fly larvae learn to recognize predators from chemical cues in the predator's diet. *Anim Behav* 52:315–320
- Clark CW, Dukas R (1994) Balancing foraging and anti-predator demands: an advantage of sociality. *Am Nat* 144:542–548
- Clutton-Brock TH, O'Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS, Manser (1999) Selfish sentinels in cooperative mammals. *Nature* 284:1640–1644
- Craig CL (1994a) Predator foraging behavior in response to perception and learning by its prey: interactions between orb-spinning spiders and stingless bees. *Behav Ecol Sociobiol* 35:45–52
- Craig CL (1994b) Limits to learning: effects of predator pattern and colour on perception and avoidance-learning by prey. *Anim Behav* 47:1087–1099
- Curio E (1976) The ethology of predation. Springer, Berlin Heidelberg New York
- Dejean A, Suzzoni JP, Schatz B (2001) Behavioral adaptations of the African ponerine ant *Plectroctena minor* (Hymenoptera: Formicidae) during the capture of millipedes. *Behaviour* 138:981–996
- Di Giusto B, Anstett MC, Dounias E, McKey D (2001) Variation in the effectiveness of biotic defence: the case of an opportunistic ant-plant protection mutualism. *Oecologia* 129:367–375
- Eickwort GC, Eickwort KR (1971) Aspects of the biology of Costa Rican halictine bees. II. *Dialictus umbripennis* and adaptations of its caste structure to different climates. *J Kans Entomol Soc* 44:343–373
- Freitas AVL, Oliveira PS (1996) Ants as selective agents on herbivore biology: effects on the behaviour of a non-myrmecophilous butterfly. *J Anim Ecol* 65:205–210
- Gill SA, Sealy SG (1996) Nest defense by yellow warblers: recognition of a brood parasite and an avian nest predator. *Behaviour* 133:263–282
- Gronenberg W, Hölldobler B (1999) Morphologic representation of visual and antennal information in the ant brain. *J Comp Neurol* 412:229–240
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Helfman GS, Winkelman DL (1997) Threat sensitivity in bicolor damselfly: effects of sociality and body size. *Ethology* 103:369–383
- Hinde R (1954) Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*): the nature of the response and the examination of its course. *Proc R Soc Lond Ser B* 142:306–331
- Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Mass
- Jackson RR, Pollard SD (1996) Predatory behavior of jumping spiders. *Annu Rev Entomol* 41:287–308
- Jeanne RL (1975) The adaptiveness of social wasp nest architecture. *Q Rev Biol* 50:267–287
- Jeanne RL (1979) A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1225
- Kojima J (1993) A latitudinal gradient in intensity of applying ant-repellent substance to the nest petiole in paper wasps (Hymenoptera: Vespidae). *Insectes Soc* 40:403–421
- Kovach WL (1994) Oriana for Windows, v. 1.0. Kovach Computing Services, Pentraeth, Wales
- Land MF (1997) Visual acuity in insects. *Annu Rev Entomol* 42:147–177
- Langley CM (1996) Search images: selective attention to specific visual features of prey. *J Exp Psychol* 22:152–163
- Levings SC, Franks NR (1982) Patterns of nest dispersion in a tropical ground ant community. *Ecology* 63:338–344
- Maloney RF, McLean IG (1995) Historical and experimental learned predator recognition in free-living New Zealand robins. *Anim Behav* 50:1193–1201
- Maschwitz U, Jessen K, Maschwitz E (1981) Foaming in *Pachycondyla*: a new defense mechanism in ants. *Behav Ecol Sociobiol* 9:79–81
- McCorquodale DB (1986) Digger wasp (Hymenoptera: Sphecidae) provisioning flights as a defence against a nest parasite, *Senotainia trilineata* (Diptera: Sarcophagidae). *Can J Zool* 64:1620–1627
- McLean IG, Rhodes G (1991) Enemy recognition and response in birds. *Curr Ornithol* 8:173–211
- Michener CD (1974) The social behavior of the bees. Harvard University Press, Cambridge, Mass
- Morse DH (1986) Predatory risks to insects foraging at flowers. *Oikos* 46:223–228
- Rosenheim JA (1990) Density-dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. *Ann Entomol Soc Am* 83:277–286
- Schatz B, Wcislo WT (1999) Ambush predation by the ponerine ant *Ectatomma ruidum* Roger (Formicidae) on a sweat bee *Lasioglossum umbripennis* in Panama. *J Insect Behav* 12: 641–663
- Schatz B, Lachaud J-P, Beugnon G (1996) Polyethism within hunters of the ponerine ant, *Ectatomma ruidum* Roger (Formicidae, Ponerinae). *Insectes Soc* 43:111–118
- Schatz B, Lachaud J-P, Beugnon G (1997) Graded recruitment and hunting strategies linked to prey weight in the neotropical ponerine ant, *Ectatomma ruidum* R. *Behav Ecol Sociobiol* 40:337–349
- Schatz B, Lachaud J-P, Beugnon G (1999) Spatio-temporal learning by the ant *Ectatomma ruidum*. *J Exp Biol* 202:1897–1907
- Skutch AF (1971) A naturalist in Costa Rica. University of Texas Press, Austin
- Stone GN (1995) Female foraging response to sexual harassment in the solitary bee *Anthophora plumipes*. *Anim Behav* 50: 405–412
- Tikkanen P, Muotka T, Hihta A (1996) Fishless-stream mayflies express behavioural flexibility in response to predatory fish. *Anim Behav* 51:1391–1399
- Tinbergen N (1960) The herring gull in its world. Doubleday, New York
- Wcislo WT (1984) Gregarious nesting of a digger wasp as a “selfish” herd response to a parasitic fly (Hymenoptera: Sphecidae; Diptera: Sarcophagidae). *Behav Ecol Sociobiol* 15:157–160
- Wcislo WT (1989) Behavioral environments and evolutionary change. *Annu Rev Ecol Syst* 20:137–169
- Wcislo WT (1992) Nest localization and recognition in a solitary bee, *Lasioglossum (Dialictus) figueresi* Wcislo (Hymenoptera: Halictidae), in relation to sociality. *Ethology* 92:108–123

- Weislo WT (1997) Behavioral environments of sweat bees (Halictinae) in relation to variability in social organization. In: Choe JC, Crespi BJ (eds) *Social behavior in insects and arachnids*. Cambridge University Press, Cambridge, pp 316–332
- Wenzel JW, Pickering J (1991) Cooperative foraging, productivity, and the central limit theorem. *Proc Natl Acad Sci USA* 88:36–38
- West-Eberhard MJ (1989) Scent-trail diversion, a novel defense against ants by tropical social wasps. *Biotropica* 21:280–281
- Wille A, Orozco E (1970) The life cycle and behavior of the social bee *Lasioglossum (Dialictus) umbripennis* (Hymenoptera: Halictidae). *Rev Biol Trop* 17:199–245
- Wisenden BD, Chivers DP, Smith RJF (1997) Learned recognition of predation risk by *Enallagma damselfly* larvae (Odonata, Zygoptera) on the basis of chemical cues. *J Chem Ecol* 23:137–151
- Zeil J, Kelber A, Voss R (1996) Structure and function of learning flights in bees and wasps. *J Exp Biol* 199:245–252