

Ambush Predation by the Ponerine Ant *Ectatomma ruidum* Roger (Formicidae) on a Sweat Bee *Lasioglossum umbripenne* (Halictidae), in Panama

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An individual ambush predation is used by huntresses of the ponerine ant *Ectatomma ruidum* to capture halictid bees (*Lasioglossum umbripenne*) in the Panamanian mountains. Workers, which use this strategy and originated from a colony (A) situated within a nest aggregation of halictid bees, capture almost four times more prey than colony (B) with a foraging area which does not include this type of bee's nest. Forty-eight percent of the prey of colony (A) are halictid bees, demonstrating the local importance of this predatory strategy in *E. ruidum*. A close examination of the behavioral sequence of predation shows that ambush is successful in only 4.8% of cases, a very low success rate in comparison to other predatory strategies described in this species. Nevertheless, due to the high repetition (16.1 ± 5.9 times on average) of very short waiting phases (6.3 ± 1.9 s), the true success rate (i.e., according to the number of individual trips) can reach up to 80%. A review of ambush predation among ant species allows us to distinguish approaches between jumping, long stealth approaches, and true ambushes. Implications of learning and expectation processes are also discussed.

KEY WORDS: Ponerinae; *Ectatomma ruidum*; ambush predation; expectation; behavioral sequence.

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INTRODUCTION

Any animal species can use an important range of foraging strategies to access its food (Bell, 1991). On the basis of the specific motility involved in the course of food searching, Pianka (1966) proposed to distinguish the sit-and-wait foragers, which await their prey in a motionless posture by ambushing, from wide-ranging foragers, which get their prey after extensive searching. Ants are well known to have developed a large variety of foraging strategies, depending on their species-specific behavioral repertoire and communication systems and on various parameters related to both the local food sources and the intrinsic characteristics of the foragers (Traniello, 1989; Hölldobler and Wilson, 1990; Schmid-Hempel, 1991). Most ant species have wide-ranging foragers, the involvement of many individuals per colony facilitating the success of this type of strategy. However, some individual foragers of some species use an ambush strategy such as dacetine ants (Wesson, 1936; Wesson and Wesson, 1939; Dejean, 1982, 1985; Masuko, 1984; Hölldobler and Wilson, 1990), *Myrmecia varians*, *M. cronata*, and *M. desertorum* (Gray, 1974) or *Ectatomma tuberculatum* (Dejean and Lachaud, 1992). Even at the collective level, *Azteca lanuginosa* use a coordinated group ambush (Morais, 1994). We present here a study of the ambush predation performed by *E. ruidum* facing a locally abundant flying prey: the halictid bee *Lasioglossum umbripenne*.

Natural History Overview of the Prey, *Lasioglossum umbripenne*

Lasioglossum umbripenne is a neotropical sweat bee, distributed from Guatemala to Venezuela (Moure and Hurd, 1987), that has been studied briefly in Costa Rica (e.g., Eickwort and Eickwort, 1971; Wcislo, unpublished data), and intensively in central Panama (Wcislo, 1997, in preparation). In Panama, activity is greatest during the dry season (mid-December to late April), diminishing during the wet season until activity ceases in the wettest months (October–November). Nests are usually found in flat, open areas, spatially clumped in nest aggregations that contain several to thousands of nests, with densities of up to 40 nests/m². Each nest has a single, constricted entrance that permits passage of only one bee at a time.

Females are very small (range of female body length = 3.9 to 5.8 mm) and usually nest in social groups that contain up to 82 females, although most colonies have many fewer bees. Most females are nonreproductive workers; one worker acts as a guard and admits nestmates, using a chemical password system. Foraging females begin work in the field at approximately 0830 and make repeated provisioning trips throughout the day. Activity peaks between 1030 and 1330, then decreases until it ceases in late afternoon. Bees learn the location of their nests, and returning bees usually enter the nest rapidly, with only a brief pause while a guard assesses whether or not the bee is a nestmate. The nest

entrance is easily recognizable because it is composed of an earthen cone with a small hole on its top (the sides of this hole often being yellow with the pollen brought back to the nest by the bee foragers).

Natural History Overview of the Predator, the Ant *Ectatomma ruidum*

The ponerine ant *Ectatomma ruidum* is a medium-sized species (range of body length = 7 to 9 mm). The monogynous colonies generally contain between 75 and 100 workers in natural conditions (Lachaud *et al.*, 1996). Distributed from the center of Mexico to southwestern Ecuador and the northern border of Brazil (Weber, 1946; Brown, 1958; Kugler and Brown, 1982), this dominant terricolous species occurs not only in coffee/cocoa plantations, maize cultures, savannas, and rain forests (Weber, 1946; Lachaud, 1990; Perfecto, 1990), but also in other biotopes like seaside, grassland, roadsides and even in city trash dumps. Its dominance can be expressed by a predatory impact estimated at 260 million prey collected per hectare per year and by a high density between 2700 and 11,200 nests/ha (Lachaud *et al.*, 1996; Schatz *et al.*, 1998b). Different authors have proposed it as an agent of biological control in cocoa and coffee plantations in Mexico (Weber, 1946; Lachaud, 1990) and in maize cultures in Nicaragua (Perfecto, 1990). Most of the time, each huntress usually forages alone on the ground within an individual foraging area (Lachaud *et al.*, 1984; Lachaud, 1985; Schatz *et al.*, in preparation). It is a diurnal species, with a triphasic activity rhythm; the peaks of activity occurring in the field at approximately 0930, 1130, and 1600 (Lachaud, 1990; Schatz *et al.*, 1994; Passera *et al.*, 1994).

Different field and laboratory studies have already demonstrated that an important foraging adaptability exists in *E. ruidum*, which is attributable to a generalist carnivorous diet (Lachaud *et al.*, 1984, 1996; Lachaud, 1990) and mainly to a large repertoire of foraging behaviors (Lachaud *et al.*, 1984; Lachaud, 1990; Schatz *et al.*, 1995, 1996, 1997, 1998a). The behavioral category of huntresses represent about 15% of workers displaying outside activities in constant laboratory conditions (Corbara *et al.*, 1989; Schatz *et al.*, 1995). While this species has been described as a solitary hunting ant (Levings and Franks, 1982; Lachaud *et al.*, 1984), several recruitment systems can gradually be employed by huntresses according to the weight and size of prey (Schatz *et al.*, 1997). Moreover, elaborate cooperation among huntresses is involved during collective predation on numerous small prey, implying a subtle within-caste specialization between stingers and transporters within huntresses (Schatz *et al.*, 1996). Cleptobiotic behavior also occurs in areas of high nest density between neighboring colonies as a facultative foraging strategy, as was observed in Costa Rica (Breed *et al.*, 1990, 1992; Jeral *et al.*, 1997), in Mexico (De Carli *et al.*, 1996, 1998), and in our study site in Panama (Schatz, personal observation); cleptobiotic behavior occurs at interspecific level too (Weber, 1946; Perfecto and Vandermeer, 1993; De Carli, 1997). In

spite of the important range of foraging strategies already described in this species (e.g., Lachaud *et al.*, 1984; Schatz *et al.*, 1997), we describe here another predatory strategy, involving an ambush waiting phase performed by huntresses of this ant species in front of halictid bees' nests. We also examine ambush behaviors among ant species and discuss involved expectation and learning processes.

METHODS

The study was conducted during March and April 1997 (latter part of the dry season) at a nest site along a dirt road running from El Llano to Cartí (7.5 km north of the Inter-Americana highway) in the Panamanian mountains, east of Panama City. Situated at an altitude of 470 m, the study site is on the side of the road crossing a recently deforested zone. An aggregation of 1555 nests of *Lasioglossum umbripenne* was encountered inside this 450-m² site (15 × 30 m). Mean density was 3.46 nests/m², but nests were not evenly distributed, the maximum observed density being 32 nests/m². We found 23 *E. ruidum* colonies in this site, i.e., a density of 511 nests/ha, which is particularly low in comparison to densities elsewhere in Panama and Mexico, which may reach more than 10,000 nests/ha (Pratt, 1989; Schatz *et al.*, 1998b).

We localized two categories of colonies: a first one constituted by six colonies, which were situated within a nest aggregation of *L. umbripenne*, and a second one constituted by seven colonies, which ignored this type of prey because they were situated outside this nest aggregation. The number of prey brought back to the nest was recorded during 1 day (from 0830 to 1630) for each of these 13 colonies. Concurrently during the same 6 days we collected the prey items brought back in one colony of each category, i.e., in a colony A (86 workers) of the first category and in a colony B (87 workers) of the second category; both colonies were about 34 m apart. Unlike workers from the colony A, those from colony B were never observed using the ambush predation and they never brought back a *L. umbripenne* as prey to the nest. In this case, each day of prey collection was separated from the other by 2 or 3 days, to avoid starving the studied colonies.

Predatory sequences were observed on 16 *E. ruidum* huntresses, originated from the same colony (Colony A). They were individually marked by color spots on their thorax and gaster, allowing each huntress to be followed easily. In all cases, the exact behavioral sequence and its total duration were recorded. The durations of 955 ambush behavior (in a motionless position) were also recorded with a minimum of 40 records per individual. By pooling the collected data, a flow diagram was devised and percentages were calculated based on the overall number of transitions between each behavioral act. The worker posture during the waiting phase was also noted. Complementary experiments were carried out to understand what kind of cues were involved in bees' nest recognition by ants.

Artificial cones were created with earth collected at the study site in respecting the shape and size of bees' nests. We observed the reaction of the huntress in 30 cases with a simple artificial cone and with other artificial cones with a hole on the top to simulate the bees' nest entrance. Thirty control experiments were also conducted with created cylinders of earth.

Otherwise, preliminary experiments allowed us to determine that *E. ruidum* workers successfully capture halictid bees essentially during the main activity period of prey. All of these observations were thus performed during that period, i.e., between 1030 and 1230. The synchronization of the activity rhythm of both prey and predator will be analyzed by considering the spatiotemporal learning ability of *E. ruidum* (Schatz *et al.* 1999a).

Statistical tests are indicated in the text. In some cases, some data are presented with a mean value, always associated with its standard deviation. Voucher specimens of both species are in the Dry Reference Collection of the Smithsonian Tropical Research Institute (Republic of Panama), the Universidad de Panama, and the Cornell University Insect Collection (Ithaca, New York).

RESULTS

Diet and Daily Prey Input

The number of workers present in colonies capturing *L. umbripennis* as prey was significantly higher than in colonies which never capture this type of prey (median value = 64.5 vs. 20 workers, respectively; Mann-Whitney test, $U = 7$; $P < 0.026$). The number of prey brought back to the nests was highly correlated with the size of the colonies ($r = 0.986$, $P < 0.001$, and $r = 0.982$, $P < 0.001$, respectively) (Fig. 1). However, the calculation of confidence intervals showed that the slopes of the two regression curves were significantly different ($P < 0.005$): colonies capturing halictid bees brought back 4.5 times more prey.

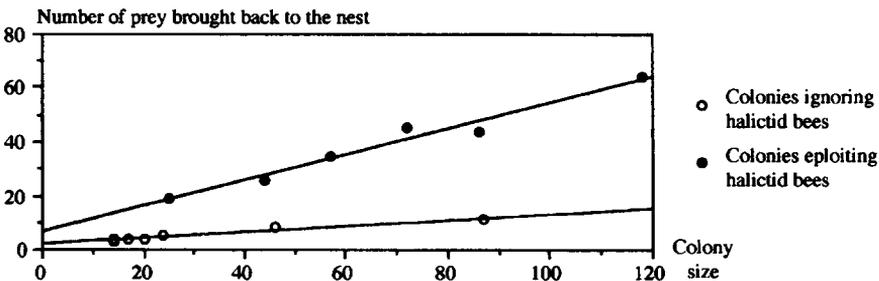


Fig. 1. Relationship between the number of prey brought back to the nest and the colony size in two categories of colonies, one ignoring halictid bees and another capturing this type of prey. All records are obtained during 1 day for each colony.

Table I. Comparison Between a Colony Ignoring Halictid Bees and Another Colony Capturing this Type of Prey During 6 Days of Prey Collection: Mean Values and Standard Deviations

Day of prey collection	Colony (B), ignoring halictid bees	Colony (A) capturing halictid bees	
	number of prey/day	Number of prey/day	Number of <i>L. umbripenne</i> /day
1	11	44	20
2	18	63	31
3	15	56	27
4	9	45	22
5	16	60	29
6	12	53	25
Total	81	321	154
Daily mean	13.50 (± 3.39)	53.50 (± 7.77)	25.67 (± 4.18)

During the same 6 days, workers from colony A (capturing *L. umbripenne* as prey) brought back 321 prey items to the nest (53.5 ± 7.8 prey/day), whereas those from colony B (ignoring this type of prey) brought back only 81 prey items (13.5 ± 3.4 prey/day), i.e., practically four times less than the first colony (Table I). This significant difference (Student test: $t = 11.6$, $P < 0.001$) was attributable mainly to the capture of *L. umbripenne*, which represented 48.0% of the number of prey items brought back to the colony A (Table I). The ambush strategy performed by huntresses facing *L. umbripenne* greatly increased the general input of prey.

Description of the Different Phases of the Predatory Sequence (Fig. 2)

The predatory sequence is described by isolating different phases of the predatory sequence as follows: search for prey, recognition of the bee «MDS»' «MDNM»s nest, ambush behavior, capture of prey, stinging of prey, and transport of prey to the nest.

Search for Prey

When the huntress exits, it immediately searches to capture either a halictid bee (by moving toward a nest of bees) or another type of prey. During the period of observation (between 1030 and 1230), the capture of other prey before the first ambush behavior occurred for only 1 of the 95 observed sequences. Both possibilities remain during the foraging trip of a huntress, because seven cases of capture of another type of prey have been observed, even after several unsuccessful ambush behaviors. Nevertheless, this situation seems to occur haphazardly when huntresses move between two bees' nests, without an active search.

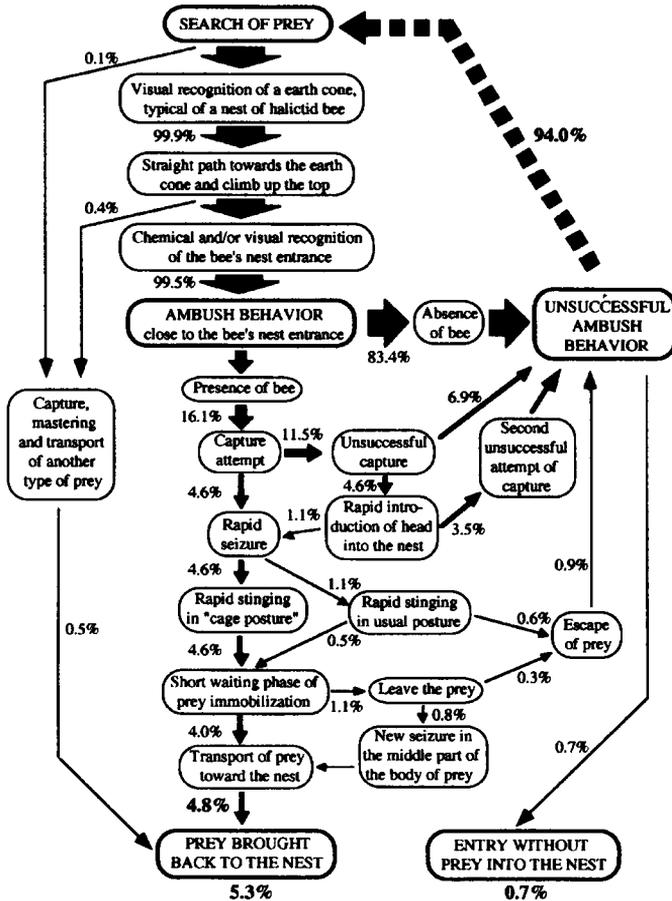


Fig. 2. Flow diagrams for the ambush predation established from the observation of the 16 marked huntresses between 1030 and 1230.

Recognition of the Bees' Nest

A foraging trip of an ambushing ant corresponds to a succession of waiting phases and paths between bees' nests. The ant moves toward a bee's nest in a generally straight line, suggesting goal orientation. By creating several artificial earth cones between different natural nests of bees (see Methods), we have observed that they are sufficient in all cases ($n = 60$) to trigger orientation behavior by ants, followed by the climbing behavior on this earth cone (cylinders of earth never triggered such a orientation in 30 cases). So the earth cone seems to be considered by ants as a visual cue associated with a nest of bees. This visual

orientation, which occurs after an unsuccessful waiting phase, is generally performed by huntresses on the top of the natural earth cone of the nest.

However, the presence of a natural entrance to the bees' nest seems to be necessary to start the waiting phase. Artificial earth cones with a hole (simulating a bee's nest entrance) ($n = 30$) or without a hole ($n = 30$) never triggered the waiting behavior by ants, even though some individuals performed antennations of holes. This result suggests that recognition of the bee's nest entrance was based on a combination chemical and visual cues.

Ambush Behavior

Huntresses always wait in front of the nest entrance, not more than 2 cm away. Motionless, the ant generally maintains its body as usual, but we sometimes observed that ants lie flat on the ground. Mandibles are opened and antennae are pointed to the nest entrance, as the usual posture adopted during nest guarding (Corbara *et al.*, 1989). This posture has been strictly adopted by 14 of 16 observed huntresses, but another waiting position has been also observed; one huntress has adopted it in all waiting phases and another in 42 of 67 cases (62.3%). It consists of an ant placing its antennae in each side of the nest entrance to seize a bee forager, which tries to leave its nest or to land close to the nest entrance. In all cases, the predation performed by *E. ruidum* on *L. umbripenne* is then based on an ambush strategy, aiming to surprise the prey.

Capture of Prey

In all cases, attempts at capture are triggered by the presence of a bee and are associated with a forward movement of the whole body of the huntress; detection, localization, approach, antennal contact, and seizure then follow in quick succession. Attempts at capture are generally observed when a bee has already landed or when a bee exits from the nest; first capture attempts are successful in 73 of 256 cases of bee presence (28.5%). In several cases, the huntress has clearly performed a capture attempt toward a bee before it lands, because its forward movement has been performed in the air and oriented toward a flying bee. It suggests a certain level of anticipation in the flight direction of a landing bee.

Two types of reaction following an unsuccessful attempt at capture are observed. In most of the cases (60.1%), the huntress goes down from the cone up to start another ambush behavior. Less frequently (39.9%), it performs a second attempt at capture by rapidly introducing its head within the nest entrance to seize either the bee which has just arrived or the bee guarding the nest entrance. This strategy is successful in only 17 of 73 cases (23.3%), and it constitutes 12 of 76 cases (15.8%) of the final number of prey items brought back to a nest. In the 256 cases where bees were present during the ambush behavior phase, suc-

successful seizures have occurred in 76 of 256 cases (29.7%) by considering both types of captures.

Stinging of Prey and Its Transport to the Nest

Huntresses immediately stung the prey after seizure, by displaying two types of posture. In only 17 of 73 cases (23.3%), prey are stung in an usual posture. The latter consists of an ant standing on its hindlegs and bending its abdomen in order to sting the prey held in its mandibles. However, huntresses have displayed another type of stinging in most of the cases (76.6%); it consists of an ant letting itself fall on one side by forming a spherical cage composed of its legs, by its bended head, by maintaining the prey in its mandibles, and by its bent abdomen to sting the prey several times. This "cage posture" is clearly associated with a successful stinging behavior, because no prey escaped in 73 cases of this type of stinging while 9 escapes are observed for 17 usual stinging behaviors. The significant difference in efficiency among the two types of stinging (Yates corrected chi-square: $\chi^2 = 37.3$, $P < 0.001$, 1 df) enables us to consider the cage posture as an "insured stinging."

In both types of stinging, huntresses have always waited for the immobilization of prey for a few seconds, before the transport phase. In most cases (79.0%; $n = 81$), motionless prey are directly transported to the nest. However, the prey was left in 21.0% of cases in order to be re-seized in the middle part of its body. Some prey escapes have occurred, and they have been significantly more frequent during this "let go and re-seize" phase (29.4%; $n = 17$) than in the course of a direct transport during which they never occurred (Yates corrected chi-square: $\chi^2 = 15.3$, $P < 0.001$, 1 df).

Other General Characteristics

The predatory sequence can be analyzed in two ways. This predatory strategy could appear as especially inefficient if we consider only one transition from "search of prey" to "transport of prey to the nest" according to the flow diagram presented in Fig. 2. The very low success rate of ambush behavior (only 4.8% of cases) can be explained mainly, on one hand, by the absence of a bee during most of the ambush phases of huntress (in 83.4% of the 1583 cases of observed ambush behaviors) and, on the other hand, by the low success rate of first capture attempts (in 28.5% of cases). However, the predatory trip should be wholly considered to account for the several repetitions of this ambush behavior performed by each huntress during the same trip. The analysis of 95 complete predatory trips shows that huntresses have brought back to the nest an halictid bee in 76 cases (in 80.0% of cases) or another type of prey in 8 cases or they have returned to their nest without prey in only 11 cases. The very low behavioral efficiency is then amply compensated by the repetition of the ambush behavior by each huntress.

A successful trip (finished by the transport of an halictid bee to the nest) is characterized by an average number of 16.1 ± 5.9 ambush behaviors per trip with a range of 6 to 32 ambush behaviors per trip. Concurrently, two types of unsuccessful trips have been distinguished. The first occurs when the huntress do not succeed to capture a bee in spite of an average value of 34.5 ± 8.5 ambush behaviors per trip ($n = 8$), a number significantly higher than during successful trips (Mann–Whitney test: $U = -4.36$, $P < 0.001$). The second type of unsuccessful trip corresponds to a particular situation: after the introduction of its head, the huntress abruptly withdraws and displays an intensive trembling attitude for several seconds. This behavior was observed in three cases and has occurred after eight, nine, and nine ambush behaviors. It has always been followed by a rapid path toward the nest, and these huntresses did not reappear for 1 or 2 days after. It suggests that the bee could display a defensive behavior, which is very effective against the ant predator.

Another important characteristic of this ambush behavior is the relatively constant duration of ambush phases; its mean value is 6.34 ± 1.89 s, with a range from 3 to 19 s in the 955 recorded cases with a minimum of 40 phases per huntress. Concurrently, the average total time of successful trips is 863 ± 355 s (or 14 min 23 s \pm 5 min 55 s), which is logically highly correlated with the number of ambush behaviors performed ($r = 0.864$, $P < 0.001$, < 74 df).

Individual Variations Within the Predatory Sequence

Individual Variation of the Ambush Posture

Two types of ambush posture have been distinguished: a usual posture adopted by 14 of 16 huntresses and a particular posture (involving antennae) strictly adopted by one huntress and in almost two-thirds of cases by another one. Huntresses wait significantly longer during this particular ambush (9.0 ± 2.3 s) than during the usual one (Student test: $t = 14.38$, $P < 0.001$) (Fig. 3A). Thus, huntresses using the usual posture of ambush ($n = 831$ cases) wait a very constant time (5.9 ± 1.4 s), which is characterized by a coefficient of variation of 24.4%. However, both categories of huntresses performed the same number of ambush behaviors before a successful bee capture (Mann–Whitney test: $z = 0.49$, $P > 0.50$) (Fig. 3B).

Individual Variation in the Reaction After an Unsuccessful Capture Attempt

Two types of reaction following an unsuccessful capture attempt have been observed: either a new ambush behavior or a rapid head introduction within the entrance of the bees' nest. However, the latter behavior has been displayed by only six huntresses: two individuals having performed it once (intermediates) and four others having performed it between 13 and 34 times (head introduction

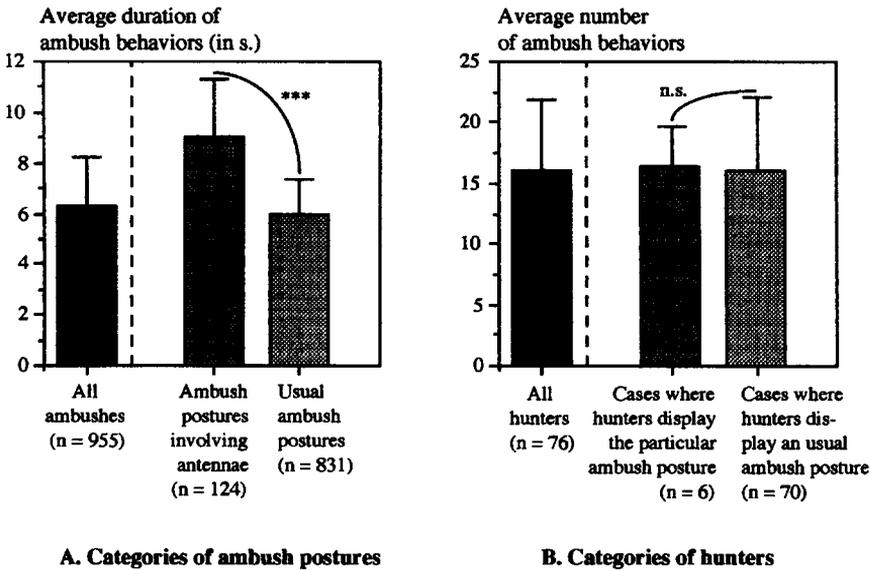


Fig. 3. Characteristics linked to both ambush postures. The characteristics of the huntress displaying both types of postures are distributed in respective appropriate categories in both figures. Comparisons are performed by using the test *t* of Student (n.s., not significant; ****P* < 0.001).

specialists) (Table II). Huntresses, displaying at least one head introduction, are as efficient as strict ambushing huntresses by considering the ratio of exits ended by the transport of a bee to the nest to the total number of exits (82.1 vs 93.6%) (Yates corrected chi-square; $\chi^2 = 1.46$, *P* > 0.10) (Table II).

Nevertheless, a more accurate analysis of the involvement of these two categories in each phase of the general predatory sequence enabled us to determine some differences. The success rate in the capture attempt is significantly higher (almost double) in strict ambushing huntresses (38.2%) than in huntresses displaying at least one head introduction (19.5%) (Yates corrected chi-square: $\chi^2 = 10.0$, *P* < 0.002) (Table II). This difference is higher by considering only the category of head introduction specialists (15.0%) ($\chi^2 = 14.8$, *P* < 0.001). Moreover, the rate of success in the capture attempt is significantly and inversely correlated with the percentage of head introductions in the category of the huntresses displaying at least one head introduction (*r* = 0.957, *P* < 0.005), even if this category is composed of only six individuals.

Huntresses, displaying the head introduction behavior, are also characterized by two other significant characteristics. They waited a slightly longer time during the ambush behavior (5.82 ± 1.39 vs. 6.07 ± 1.50 ; Student test, *t* = 2.51, *P* < 0.02) (Fig. 4A). However, this small difference cannot be interpreted be-

Table II. Behavioral Differences Among the Three Categories of Huntresses in Success Rates, Capture Attempts and Transport of a Bee to the Nest, and in the Reaction After an Unsuccessful Capture Attempt^a

Individual	Success rates		Reaction after an unsuccessful capture		
	Attempts of capture	Transport of a bee to the nest	New ambush	Head introduction	Percentage of head introduction
Strict ambushing huntresses (<i>n</i> = 10)	38.2% (47/123)	93.6% (44/47)	82	0	0.0%
Intermediate (<i>n</i> = 2)	45.0% (9/20)	38.2% (9/10)	9	2	8.2%
Head introduction specialists (<i>n</i> = 4)	15.0% (17/113)	79.3% (23/29)	25	71	74.0%
Total of huntresses displaying at least one head introduction (<i>n</i> = 6)	19.5% (26/133)	82.1% (32/39)	34	73	68.2%

^aWe have distinguished three categories of workers: "strict ambushing huntresses," "intermediates" (displaying one head introduction), and "head introduction specialists" (performing this behavior from 10 to 27 times). The latter two categories are pooled in "huntresses displaying at least one head introduction."

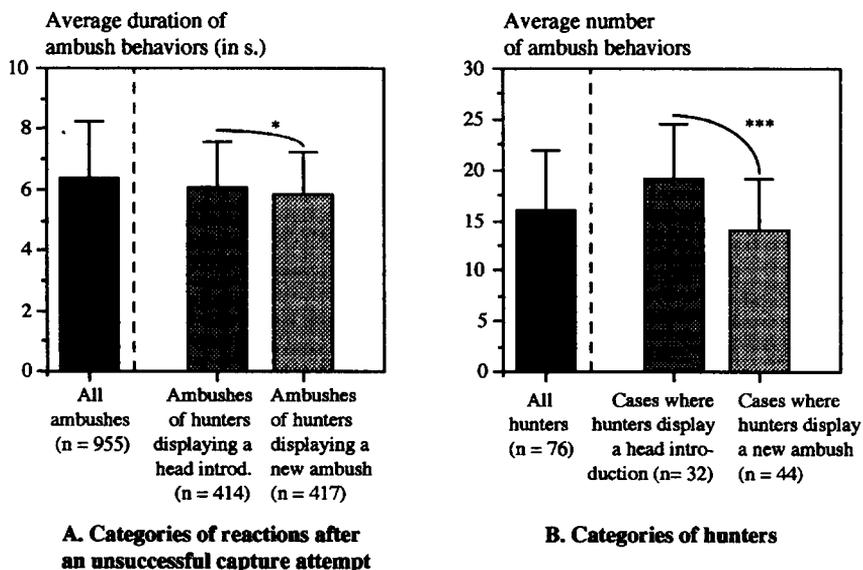


Fig. 4. Characteristics linked to both reactions after an unsuccessful capture attempt. The duration of ambush behaviors (A) is calculated on 831 ambushes, by excluding those performed by the two huntresses displaying the particular ambush posture, because they are characterized by an extended waiting phase. Comparisons are performed by using the test *t* of Student (**P* < 0.02; ****P* < 0.001).

cause the accuracy during our time records was only 1 s. But they have displayed a significantly higher number of ambush behaviors before transporting the bee up to the nest (13.93 ± 5.22 vs. 18.96 ± 5.65 ; $t = 3.96$, $P < 0.001$) (Fig. 4B). Third, successful exits of huntresses displaying head introduction have logically lasted a slightly longer time (980.3 ± 323.3 vs. 777.7 ± 351.4 s; $t = 2.57$, $P < 0.02$).

Furthermore, the specialization of head introduction after an unsuccessful attempt at capture is also associated with particular behaviors in the next steps of the predatory sequence. Huntresses displaying head introduction have also stung their prey in the usual posture significantly more often than in cage posture (Yates corrected chi-square: $\chi^2 = 25.15$, $P < 0.0001$). Performing the usual posture, they have also performed slightly more new seizures of prey before the transport phase (Yates corrected chi-square: $\chi^2 = 6.46$, $P > 0.02$). Thus, contrary to the first individual variation, this one is clearly associated with significant numerous variations of predatory behavior. Otherwise, huntresses, displaying the particular ambush posture, have been observed performing new ambushes after an unsuccessful ambush and stinging in a cage posture, and then, both types of individual specializations are not associated.

DISCUSSION

The term "ambush" is often used to describe a predatory strategy, where huntresses do not display a direct approach towards the prey. However, a review of the "indirect approaches" in ant species allows us to distinguish three categories of "ambushes": jumping strategy, stealth approach, and real ambush (Table III). As in the case of the Salticidae or other "jumping spiders," the jumping strategy pools various types of predation started by remote perception of prey, followed either by a remote stealth approach or by taking a good jump position, rapidly followed by a "jump" toward the prey and ended by a rapid capture attempt of prey. The jump could be horizontal as in *Harpegnathos* sp. (Crosland, 1995; Musthak Ali *et al.*, 1992), more or less vertical in the cases of jumping from a branch as in *Myrmecia* sp. (Gray, 1974) or strictly vertical in the case of deliberate free fall from trees and bushes encountered in many formicine species (reviewed by Hölldobler and Wilson, 1990).

The stealth approach seems closely associated with the holder of the trap-jaw system. After haphazard encounter of prey, long-mandibulate huntresses generally stop walking, lower against the substratum, open their mandibles, turn to face the prey, and advance cautiously before seizure and stinging (Dejean, 1982; Masuko, 1984). The duration of stealth approach is variable among long-mandibulate species, while short-mandibulate ones more cautiously approach the prey (Wilson, 1953; Brown and Wilson, 1959; Masuko, 1984). Moreover, some short-mandibulate species and intermediate ones display a body-smearing behavior (Wesson and Wesson, 1939; Dejean, 1982; Masuko, 1984) certainly to

Table III. Review of the Different Categories of "Indirect Approaches" During Predation in Ants

Type of approach	Ant species	Characteristics of predation	Authors
Jumping	Ponerinae <i>Harpegnathos saltator</i> , <i>Harpegnathos venator</i>	Jumping near the prey after a stealth approach	Crosland, 1995; Musthak Ali <i>et al.</i> , 1992
	Myrmicinae (Dacetini) <i>Orectognathus</i> sp.	Jumping near the prey	Carlin, 1981
	Myrmeciinae <i>Myrmecia varians</i> , <i>M. cronata</i> , <i>M. desertorum</i>	Jumping near the prey after a stealth approach	Gray, 1974; Eriksson, 1985
	Nothomyrmeciinae <i>Nothomyrmecia Macroes</i>	Jumping near the prey after a stealth approach	Hölldobler and Taylor, 1983
Long stealth approach	Ponerinae <i>Anochetus</i> sp., <i>Odontomachus troglodytes</i>	Short mandibles with a trap-jaw system Long mandibles with a trap-jaw system	Brown, 1976 Dejean and Bashingwa, 1985
	Formicinae <i>Myrmoteras toro</i>	Long mandibles with a trap-jaw system, short stealth approach	Moffett, 1986
	Myrmicinae (Dacetini) <i>Strumigenys</i> sp., <i>S. lewisi</i> , <i>S. solifontis</i> , <i>S. louisianae</i> , <i>S. rufobrunea</i>	Long mandibles with a trap-jaw system	Wesson, 1936; Brown and Wilson, 1959; Dejean, 1982; Masuko, 1984; Hölldobler and Wilson, 1990
	<i>Pentastruma canina</i> , <i>Labidogenys</i> sp., <i>Epitrirus hexamerus</i>	Short mandibles with a trap-jaw system	Wesson and Wesson, 1939; Dejean, 1982, 1985
	<i>Smithistruma emarginata</i> , <i>S. truncatidens</i> , <i>S. rostrata</i>	Intermediate mandibles with a trap-jaw system	Dejean, 1982
	<i>Serrastruma serrula</i>	Short mandibles with a trap-jaw system	Wilson, 1953
	<i>Trichoscapa membranifera</i>	Short mandibles with a trap-jaw system	Wilson, 1953
True ambush	Ponerinae <i>Ectatomma ruidum</i>	Motionless posture	Dejean and Lachaud, 1992
	<i>Ectatomma ruidum</i>	Motionless posture facing prey nest entry	This study
	<i>Ectatomma ruidum</i>	Motionless posture facing prey nest entry	This study

Table III. Continued

Type of approach	Ant species	Characteristics of predation	Authors
	<i>Ectatomma tuberculatum</i>	Motionless posture	Dejean and Lachaud, 1992
	<i>Pachycondyla</i> sp., <i>Paltothyreus</i> sp.	Hiding under leaves and debris	Reviewed by Hölldobler and Wilson, 1990
	Dolichoderinae	Coordinated group ambush displayed under a leaf	Morais, 1994
	<i>Azteca</i> cf. <i>lanuginosa</i>		
	Myrmicinae (Basicerotini)	Camouflaging behavior and anatomy	Wilson and Hölldobler, 1986
	<i>Basiceros manni</i> , <i>Octostruma</i> , <i>Eurhopalothrix</i> , <i>Protalaridis</i>		

deceive the prey, by concealing the ant's odor with surroundings (Masuko, 1984). Further, the body of some species, like *Epitritus hexamerus* and *Labidogenys* sp. (Masuko, 1984; Hölldobler and Wilson, 1990), is covered with a curious pilosity, which could serve as tactile lures (Brown, 1950; Wilson, 1953).

Both first categories correspond to predatory strategies started after the prey perception and are differentiated by subtle differences in approach of prey, which are generally encountered haphazardly. Conversely, the third category of ant predators corresponds to a true ambush behavior, because huntresses wait for prey before they perceive them. Sophisticated strategies are generally involved according to environmental characteristics. In the arboreal ant *Azteca* cf. *lanuginosa*, a group of huntresses waits under a leaf margin by spacing themselves evenly, attacks simultaneously prey that land on a leaf, carry it to the lower surface of the leaf, and dismembers it before its transport to the nest (Morais, 1994). In the terricolous ant *Basiceros manni*, the "slowest-moving" ant is equipped with different types of hairs, where it accumulates fine particles of soil to increase its camouflage (Wilson and Hölldobler, 1986). However, as pointed out by different authors in various animal species (Krebs *et al.*, 1974; Curio, 1976; Charnov, 1976; Davis, 1977), the problem for a true ambusher to solve is to select an optimal ambush site in order to increase its predatory efficiency. In this way, *Ectatomma ruidum* huntresses wait close to the prey nest entrance in a motionless posture and repeat these ambushes until they successfully capture a prey. Among true ambushers within ant species, *E. ruidum* is the only one to perform repeated ambushes, this fact probably being due to the local high abundance of a potential prey, the halictid bee *Lasioglossum umbripenne*. Displayed only in true ambusher ants, the ability to start a waiting phase while the prey is

absent clearly suggests that huntresses are able to associate particular sites with a potential availability of prey, as demonstrated in birds or mammals (Krebs *et al.*, 1974; Curio, 1976; Charnov, 1976; Davies, 1977). Moreover, waiting close to the bees' nest entrance allows *E. ruidum* huntresses to avoid expending considerable energy in the pursuit of prey, as proposed for the spotted flycatcher or for other sit-and-wait predators (Curio, 1976; Davies, 1977).

Ecological Importance of Ambush predation

Brief observations at other nesting sites, hundreds of kilometres from our site, indicate that the ambush strategy of *Ectatomma* might be widely used. In Panama, we have observed such behavior at a *L. umbripennis* site in far western Panama (Chiriqui Province), and another near the Atlantic coast, east of Colon (Colon Province); at a nesting site of sphecid wasp (*Trachypus petiolaris*); and at nesting sites of another halictid, *Halictus hesperus*, on Taboga Island (Panama Province) and at Lago Mar (Cocle Province). The nest of *H. hesperus* is shaped like a volcano, topped by a little hollow (diameter: 1 cm), with the entrance at the bottom of the hollow (photos of nest entrances are given by Brooks and Roubik, 1983). We hypothesize that the hollow provides a small barrier between predator and prey, decreasing predator efficiency by increasing predator-prey distance. In Brazil, *Ectatomma* have been observed hunting another halictid bee, *Pseudagapostemon* (D. Yanega, personal communication). All these observations illustrate the fact that ant predation represents an important cost to social groups of halictid bees, which are usually characterized by a small number of individuals, as in the case of a *L. umbripennis* nest (Alexander, 1974; Wcislo, 1997).

We demonstrate that the presence of nest aggregation of *L. umbripennis* is associated with the increased size of *E. ruidum* colonies capturing this halictid bee as prey. The food supply, constituted by the large number of captured sweat bees, is likely to induce a worker production [which require about 1 month (Schatz *et al.*, in preparation)] even if bees' nests are usually rebuilt each year by the foundress and if annual activity of bees is reduced to 4.5 months per year. During this period, the use of ambush predation in *E. ruidum*, already found on rare occasions in Mexico (Dejean and Lachaud, 1992), here appears as a stable strategy, as described in another species of the same genera: *E. tuberculatum* (Dejean and Lachaud, 1992). The prey collection performed at the end of the dry season showed that prey of *E. ruidum* were constituted almost half by *L. umbripennis*, demonstrating the important impact of this ambush strategy in the diet of this ponerine ant usually more eclectic (Lachaud, 1990; Lachaud *et al.*, 1984, 1996). These results also illustrate the fact that the richness of food sources must be analyzed at the level of colony foraging area to account for local heterogeneities, considering the differences in prey quantities brought back by huntresses of the two categories of studied colonies.

Behavioral Sequences

The ambush predation is associated with the display of several predatory behaviors by *Ectatomma ruidum* huntresses. Several predatory acts are common with the sequence used by this species facing nonflying prey, for instance, larvae of mealworms (*Tenebrio molitor*) or earthworms (Schatz *et al.*, 1997). First, as in numerous other examples in ants (Agbogba, 1982; Dejean *et al.*, 1993; Schatz *et al.*, 1997), the mobility of prey is necessary to start stinging, because this behavior never occurs in fields with dead bees, which are sometimes discovered by chance by huntresses. Second, the stinging is always followed by a waiting phase of prey immobilization, even if its duration seems shorter than in the case of larger prey. And third, the "let go and re seize" phase happens again before the start of the transport phase and is always associated with a new seizure in the middle part of the prey body.

Concurrently, two new types of predatory behaviors are also observed: ambush postures and the stinging in "cage posture." Both types of ambush posture are characterized by a motionless position, open mandibles, and antennae pointed to the nest entrance, as described in several other ant species performing ambushes (Wesson, 1936; Dejean, 1982; Masuko, 1984; Holldobler and Wilson, 1990). In contrast with predation observed facing walking prey, this posture is displayed during the absence of prey when the huntress expects an encounter with it, as already observed facing live fruit flies (*Drosophila*) placed in a regularly supplied predation site (Schatz *et al.*, 1996). Two of sixteen observed huntresses have adopted a particular ambush posture, where individuals lie flat on the ground and place its antennae in each side of the nest entrance. It is probable that this extreme ambush posture enables huntresses to reduce their visibility, especially toward a bee exiting from its nest. As in the case of other opportunist ambushers in the animal kingdom who do not have morphological adaptations of concealment or camouflage, the motionless and crouching ambush posture corresponds to a way of minimizing their visibility facing the prey and maximizing the efficiency of the final assault (Curio, 1976).

The second new behavior concerns the stinging behavior displayed in most cases in a "cage posture," which is clearly associated with a significant decrease of prey escape in comparison with those occurring during usual stinging. The cage posture stinging has been also frequently observed during the predation of live fruit flies but never with mealworms (Schatz, personal observation). Two other strategies allowing to master a flying prey were described within ant species; huntresses of *Paltothyreus tarsatus* can learn in a few trials to capture butterflies by using their forelegs in addition to their mandibles (Dejean *et al.*, 1993). In *Oecophylla longinoda*, when a huntress succeeds to capture a *Drosophila* fly, nestmates rapidly arrive in order to collectively spreadeagle it for several minutes; the prey lost its reflexes and will then be transported to the nest

by a single worker (Dejean, 1990). When faced with small flying prey, huntresses of *E. ruidum* are able to associate an escape risk with this type of prey and to adopt a behavior to "insure stinging"; this ability had also been pointed out in short-mandibulate dacetines ants (Masuko, 1984). In addition to their ability to perceive a mortality risk associated with large and heavy prey (Schatz *et al.*, 1997), huntresses of *E. ruidum* are thus able to display three types of stinging (usual, prudent, and insured stinging), especially adjusted to prey characteristics.

Individual Variation in Predatory Sequences

Individual variations have been demonstrated in the ambush posture and in the reaction after an unsuccessful capture attempt. In contrast to the first one, the second type of individual variation in predatory behavior was associated with a series of subsequent behaviors (more stinging in usual posture and more new prey seizure before its transport). Several characteristics in the efficiency predation (less efficiency in the capture attempt, a higher number of ambush behaviors, and a higher duration of predatory trips before successfully transporting a prey to the nest) suggest that huntresses, displaying head introduction, and are less efficient than strict ambushing huntresses. It is probable that the ambush predation in *E. ruidum* can be progressively acquired in the course of individual successive trips, as described in other ponerine species, *E. tuberculatum* (Dejean and Lachaud, 1992), *Paltothyreus tarsatus* (Dejean *et al.*, 1993), and *Odontomachus troglodytes* (Dejean and Lachaud, 1991) and in the myrmicine ant, *Smithistruma emarginata* (Dejean, 1985). In this way, huntresses displaying head introductions would correspond to individuals recently involved in predation (with different levels of efficiency) and strict ambushers to individuals with a relatively high experience in this predatory strategy. Moreover, according to the model developed for *Pachycondyla apicalis* by Deneubourg *et al.* (1987), a high activity rate is likely to affect the mechanism of individual specialization: the greater number of ambushes repetition leading to a stronger level of specialization in individual predatory sequences. This could explain why most huntresses are highly specialized in predatory sequences composed of successive ambushes (without head introduction), stinging in cage posture, and prey transports without a "re seizure" phase.

Expectation Phenomenon and Learning Processes

In all the descriptions of the use of a sit-and-wait strategy in ant species, huntresses wait a long period of time at the same site before or after prey perception; the waiting period can generally last tens of minutes, as in *Smithistruma rostrata* (Wesson and Wesson, 1939), *Strumigenys* spp. (Dejean, 1982), *Epitri-*

tus hexamerus (Masuko, 1984), or *Azteca* cf. *lanuginosa* (Morais, 1994), and even 2 or 3 h in *Ectatomma tuberculatum* (Dejean and Lachaud, 1992). The efficiency of such a long waiting period at one site is directly associated with the local richness of prey, as it is the case for web spiders or ant lions (Curio, 1976), and according to the rate expectation hypothesis proposed by Charnov (1976). Regarding the duration of waiting phases, the case of ambush predation performed by *E. ruidum* huntresses seems to be unique in ants, because their waiting periods are characterized by a short duration (about 6 s), by a low variability (with low intra- and interindividual variations) and by a change of waiting site after each ambush. A similar ambush type was encountered in two bird species, the black-capped chickadee *Parus atricapillus* and the spotted flycatcher *Muscicapa striata*, which display sequences of several ambushes characterized by a short constant duration (about 11 and 30 s, respectively) and by changing of waiting site (Krebs *et al.*, 1974; Davies, 1977). Such an ambush strategy suggests that individuals are able to estimate the duration of ambush in short term and that they learn to spend this constant amount of time per site, as pointed out in birds by Krebs *et al.* (1974) and Davies (1977). In spite of its invertebrate status, both abilities in mastering of temporal information have been already demonstrated in *E. ruidum* foragers during temporal and spatiotemporal learning of food availability periods (Schatz *et al.*, 1994, 1999a; Beugnon *et al.*, 1996; Schatz, 1997).

Concurrently, straight paths between cones and recognition of artificial earth cones suggest huntresses have learned to recognize earth cones as the same visual landmark associated with bees' nests, such abilities in visual learning being already demonstrated in *E. ruidum* in various foraging situations (Jaffe *et al.*, 1990; Schatz *et al.*, 1994, 1995; Schatz, 1997). Moreover, huntresses have also learned to consider halictid bees as prey associated with a high escape risk, and probably to adopt not only "insured stinging," but also very rapid capture attempt and short waiting of prey immobilization. A similar type of learning has been demonstrated in *E. ruidum*, where huntresses have associated a mortality risk with vigorous large and heavy prey (Schatz *et al.*, 1997), but also in various other ant species (Nonacs, 1990; Dejean *et al.*, 1990, 1993). Such huntresses' learning abilities are closely related with foraging efficiency (Traniello, 1989; Johnston, 1991) and, more especially, with the rate success of predation (Dejean *et al.*, 1990, 1993; Schatz *et al.*, 1997). These learning abilities of *E. ruidum* once again reinforces the important flexibilities of its predatory behavior already pointed out in previous reports (Lachaud *et al.*, 1984; Breed *et al.*, 1990; Beugnon *et al.*, 1996; Schatz *et al.*, 1997, 1998a, 1999a, b). Such a flexibility in foraging strategies may permit the utilization of alternative food sources by specialized species (Dejean, 1982; Dejean *et al.*, 1999; Lachaud and Dejean, 1994) or the exploitation of a wider range of food items by generalist species (Hölldobler, 1984), as in the case of *E. ruidum* (Schatz *et al.*, 1997).

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