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Prey Density and Polyethism within Hunting Workers in the Neotropical Ponerine Ant *Ectatomma ruidum* (Hymenoptera, Formicidae)

by

B. Schatz¹, J.P. Lachaud^{1,2}, G. Beugnon¹ & A. Dejean³

ABSTRACT

When supplied with numerous live prey, hunting workers of the Neotropical ant *Ectatomma ruidum* can be subdivided into two categories: "stingers" specialized in killing prey and "transporters" specialized in taking them one by one to the nest. We examined here how the division of labor between the hunting workers is affected when different quantities of prey are supplied, and whether this response is associated with a perception of different total numbers of prey or different densities of prey. In seven colonies of different sizes, the increasing quantity of prey supplied was associated with an increase in the number of stingers from minimal to maximal values between which these two parameters were highly correlated. Moreover, there were significant positive correlations between colony size and the minimal or maximal value of the number of stingers. Whatever the colony size, when the number of stingers reached its maximal values, the proportion of workers in each behavioral subcaste of hunting workers was stable. Concurrently, a series of tests, where the number of prey, their density and the surface of the predation site were alternatively maintained constant, indicated that each hunting worker estimated the "quantity of prey" according to their density at the predation site, and not according to their total number.

Key words: Predation, quantity estimation, hunting workers polyethism, colony size, Ponerinae

INTRODUCTION

In the animal kingdom, ants are well known to have developed in the course of their evolution a large variety of foraging strategies depending notably on their species-specific behavioral repertoire and on various characteristics of food sources (Curio 1976, Traniello 1989, Hölldobler

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& Wilson 1990, Peeters 1997). Obviously, the more flexible the foraging behavior, the more readily colonies can adjust their adaptive response to environmental changes. Several cases of such shifts in foraging strategies have been reported in ants; for example, harvester ants react to seed density (Bernstein 1975), *Serrastruma serrula* and *S. lujae* to the number of prey supplied (Dejean 1987, Dejean & Benhamou 1993) and *Paraponera clavata* and *Ectatomma ruidum* to prey size (Breed *et al.* 1987, Schatz *et al.* 1997). For generalist predatory species, an important variety of predatory strategies represents a clear ecological advantage since it allows to take advantage of a wide range of potential prey (Dejean & Corbara 1990; Dejean *et al.* 1993; Lachaud & Dejean 1994; Schatz *et al.* 1997). Besides such a variety in the kind of strategy used, certain ant species are also able to display an important flexibility within a given strategy, as recently demonstrated for the workers of *Myrmicaria opaciventris* which can match the number of hunters involved in cooperative predatory behavior to the prey size (Dejean *et al.* 1999).

The hunting workers of the Neotropical ponerine ant *Ectatomma ruidum*, forage essentially solitarily (Lachaud *et al.* 1984; Lachaud 1985) but are able to exhibit both kinds of predatory behavior flexibility. Such a flexibility can result in cooperative predatory behaviors and even in a sophisticated graded recruitment (Schatz *et al.* 1997) linked to prey weight and size. Nevertheless, field and laboratory experiments have shown that other parameters, linked to the quantity of prey or of food-sources, could be involved. The kinetics of the individual predatory behavior can be influenced by the number of food-sources available and the quantity of prey supplied at each source (Lachaud *et al.* 1990). Moreover, as in the African ponerine ant *Pachychondyla caffraria* (Agbogba & Howse 1992), when numerous live prey are available, a group of hunters (the "stingers") specialized in killing successive prey and another group (the "transporters") in carrying the dead prey one by one back to the nest (Schatz *et al.* 1996).

In this paper, we attempted to investigate how the hunters of *E. ruidum* can adjust their collective predatory behavior in accordance with variations in the quantities of prey supplied. We conducted experiments on seven colonies of different sizes in order to determine in what ways the number and the proportion of workers involved in the two behavioral subcastes of hunting workers might vary according to large increase in the prey number. Secondly, we investigated two hypotheses which might explain how hunting workers are able to estimate either the total number of prey or the density of prey.

MATERIALS AND METHODS

Experimental conditions

Ectatomma ruidum is a dominant terricolous species (Lachaud 1990, Schatz *et al.* 1998b), common in coffee or cocoa plantations of Central America, where it preys on a large variety of arthropods (membracids, crickets, flies and termites) (Weber 1946, Lachaud, 1990) while some foragers specialize in honey-collecting (Schatz *et al.* 1995). Seven colonies of *E. ruidum* of different sizes, collected at Rozario Izapa (Chiapas, Mexico), were reared in plaster nests placed in an experimental room under controlled conditions (temperature: $25^{\circ} \pm 1^{\circ}\text{C}$; humidity: $60\% \pm 5\%$; photoperiod: 12:12 L/D). Hunting workers were offered fruit flies (*Drosophila melanogaster*) as prey. The experimental set-up was composed of a foraging area (30 x 30 cm) connected at one end to the nest and at the other end to the hunting area, which had five different sizes. The smallest hunting area was a petri dish measuring 52.8 cm^2 (8.2 cm in diameter and 1 cm in height). The four others, made with plasticine walls (1 cm in height) covered by a plate of glass were made in order to measure two, three, four and five times the surface of the petri dish (105.6 cm^2 , 158.4 cm^2 , 211.2 cm^2 and 264.0 cm^2 , respectively). For each test, the prey were provided in the hunting area (about 35 cm from the nest entrance) and observations started when the first prey item was captured by hunting worker.

Experiment 1: effect of the quantity of prey supplied

Nine different quantities of prey were chosen according to the size of each colony, and up to 12 in the case of colony F (**Table 1**). The tests were performed each 3 or 4 days by alternating small and large quantities of prey to avoid any effect linked to the expectation of a certain quantity of prey and to the saturation of the colonies (Schatz 1997). All tests for experiment 1 were performed using a petri dish (52.8 cm^2) as a hunting area. During preliminary experiments, all hunting workers coming into the hunting area were individually marked with spots of colored enamel paint on their thorax and gaster. For each test, we recorded all killing and transporting acts performed by each marked ant present in the hunting area every 10 minutes until 90% of prey were killed or over a maximum 2-hour period.

Experiments 2 and 3: Determination of the "quantity of prey" by the hunting workers

Experiments 2 and 3 were performed on colony F in order to test whether the collective organization of hunting workers varies according to the perceived total number of prey or to the perceived density of prey.

For each experiment, two out of three parameters (surface of the predation site, quantity of prey and density of prey) varied while one parameter remained constant (Table 2). Experiment 2 (tests 6 to 9) consisted in keeping the prey density constant (1.5 prey/cm²) while the quantities of prey supplied varied. Experiment 3 (tests 10 to 13) was performed by keeping the number of prey supplied constant (400 prey) and by varying the density of prey. These two experiments were possible due to the use of hunting areas of different sizes. We also reported in Table 2 some results on colony F from experiment 1 (tests 1 to 5) which were used as control tests.

RESULTS

Experiment 1: Adjustment between the quantity of prey and the number of stingers

For each colony the total number of hunting workers increased slowly according to the quantity of prey supplied. For very high prey quantities, the maximal number of hunting workers was proportional to the colony size (linear positive correlation: $r = 0.988$; 6 df; $p < 0.0001$) (Fig. 1A). Nevertheless, the correlation between the proportion of hunting workers and the colony size was highly negative (logarithmic negative correlation: $r = 0.939$; 6 df; $p < 0.001$) (Fig. 1B).

The increase in the quantity of prey supplied was associated with an increase in the relative number of stingers according to two rules, as demonstrated by the example of colony F (Fig. 2). (1) The variation in the number of stingers was comprised between minimal and maximal values (four and 12 stingers, respectively, for colony F). (2) Between these two values, the number of stingers was highly correlated with the number of prey (or their density) (linear positive correlation: $r = 0.993$; 6 df; $p < 0.0001$). The equation of this correlation curve allowed us to establish that the number of stingers was minimal for prey quantity

Table 1 : Sequential order of the quantities of prey supplied during each test for the seven studied colonies.

| N° Colony | Colony size | Range of the quantities of prey supplied | 1st test | 2nd test | 3rd test | 4th test | 5th test | 6th test | 7th test | 8th test | 9th test | 10th test | 11th test | 12th test |
|-----------|-------------|--|----------|----------|----------|----------|----------|----------|----------|----------|----------|-----------|-----------|-----------|
| A | 24 | 10 to 100 | 30 | 20 | 40 | 15 | 50 | 10 | 100 | 60 | 80 | / | / | / |
| B | 60 | 30 to 300 | 120 | 100 | 150 | 80 | 200 | 50 | 300 | 30 | 250 | / | / | / |
| C | 109 | 60 to 300 | 150 | 120 | 200 | 100 | 250 | 80 | 300 | 60 | 70 | / | / | / |
| D | 130 | 60 to 350 | 200 | 150 | 250 | 120 | 300 | 100 | 350 | 60 | 80 | / | / | / |
| E | 160 | 70 to 350 | 200 | 150 | 250 | 120 | 300 | 100 | 350 | 70 | 80 | / | / | / |
| F | 240 | 50 to 700 | 240 | 200 | 300 | 150 | 400 | 120 | 500 | 100 | 600 | 80 | 700 | 50 |
| G | 350 | 80 to 700 | 300 | 250 | 400 | 200 | 500 | 150 | 600 | 80 | 120 | 700 | / | / |

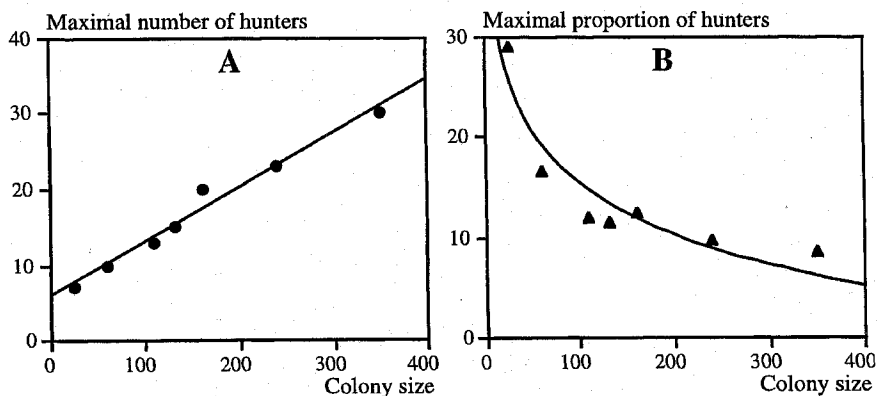


Fig. 1: Relationships between colony size and the maximal number of hunting workers (A) or the maximal proportion of hunting workers (B).

Table 2 : Program of the three series of tests (see text). In each series, one parameter was maintained constant (bold) while the two others varied (standard).

| Experiment 1: constant surface, variable number and density of prey | | | Experiment 2: constant density of prey, variable surface and number of prey | | | Experiment 3: Constant number of prey, variable surface and density of prey | | |
|--|--|--|--|---|--|--|--|--|
| N° | Values of test parameters | Values of parameters compared to test n°1 | N° | Values of test parameters | Values of parameters compared to test n°1 | N° | Values of test parameters | Values of parameters compared to test n°1 |
| 1 | 80 prey 52.8 cm² 1.5 prey/cm ² | N1 S1 D1 | 1 | 80 prey 52.8 cm ² 1.5 prey/cm² | N1 S1 D1 | 5 | 400 prey 52.8 cm ² 7.6 prey/cm ² | 5 x N1 S1 5 x D1 |
| 2 | 150 prey 52.8 cm² 2.8 prey/cm ² | 1.88 x N1 S1 1.88 x D1 | 6 | 160 prey 105.6 cm ² 1.5 prey/cm² | 2 x N1 2 x S1 D1 | 10 | 400 prey 105.6 cm ² 3.8 prey/cm ² | 5 x N1 2 x S1 2.5 x D1 |
| 3 | 240 prey 52.8 cm² 4.5 prey/cm ² | 3.13 x N1 S1 3.13 x D1 | 7 | 240 prey 158.4 cm ² 1.5 prey/cm² | 3 x N1 3 x S1 D1 | 11 | 400 prey 158.4 cm ² 2.5 prey/cm ² | 5 x N1 3 x S1 1.67 x D1 |
| 4 | 300 prey 52.8 cm² 5.7 prey/cm ² | 3.75 x N1 S1 3.75 x D1 | 8 | 320 prey 211.2 cm ² 1.5 prey/cm² | 4 x N1 4 x S1 D1 | 12 | 400 prey 211.2 cm ² 7.9prey/cm ² | 5 x N1 4 x S1 1.25 x D1 |
| 5 | 400 prey 52.8 cm² 7.6 prey/cm ² | 5 x N1 S1 5 x D1 | 9 | 400 prey 264.0 cm ² 1.5 prey/cm² | 5 x N1 5 x S1 D1 | 13 | 400 prey 264.0 cm ² 1.5 prey/cm ² | 5 x N1 5 x S1 D1 |

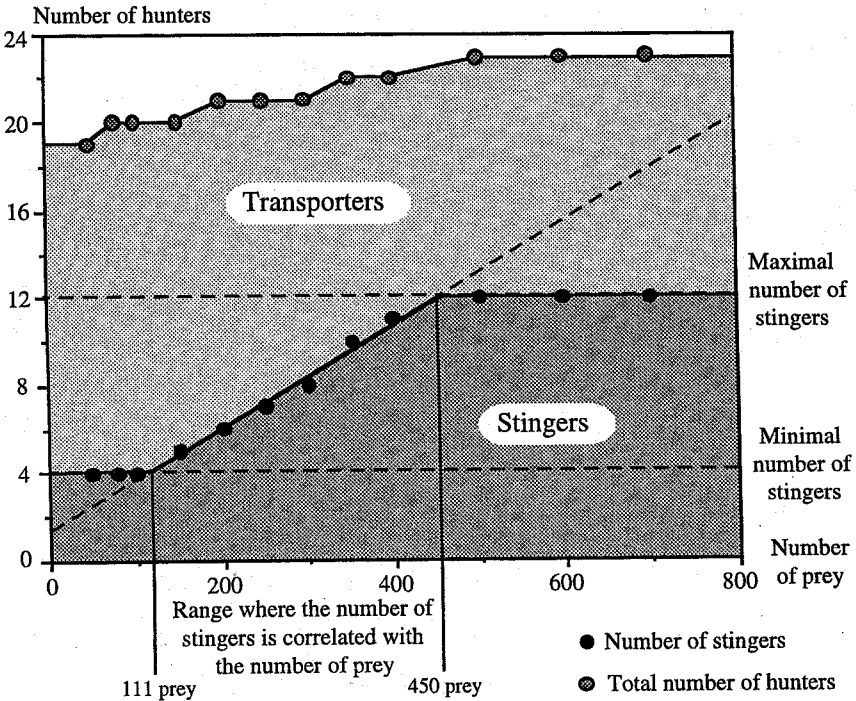


Fig. 2: Variations in the numbers of stingers and transporters according the quantity of prey supplied to colony F.

values lower than 111 prey and maximal from values higher than 450 prey.

Both rules interestingly apply to the six other colonies, whatever their size. The increasing quantity of prey supplied was associated with an increase in the number of stingers between minimal and maximal values. (1) Between these two values, both parameters were highly correlated ($p < 0.001$) (Fig. 3). In spite of the proximity between the size (24 workers) of the smallest colony and the critical size ($n = 18.4$) at which one stinger appears among hunting workers in 50% of the cases (Schatz *et al.* 1998a), a variation in the number of stinger was noted. However, because this variation was too small, a correlation curve was not calculated for the smallest colony.

The minimal value of stingers was considered when the number of prey was at its highest limit before any increase in the number of stingers and the maximal value for this behavioral subcaste was considered when the number of prey was at its lowest limit corresponding to the stabilization of the number of stingers. The maximal value of the number of stingers was on average 2.4 times (min.-max.: 2.0 to 3.0)

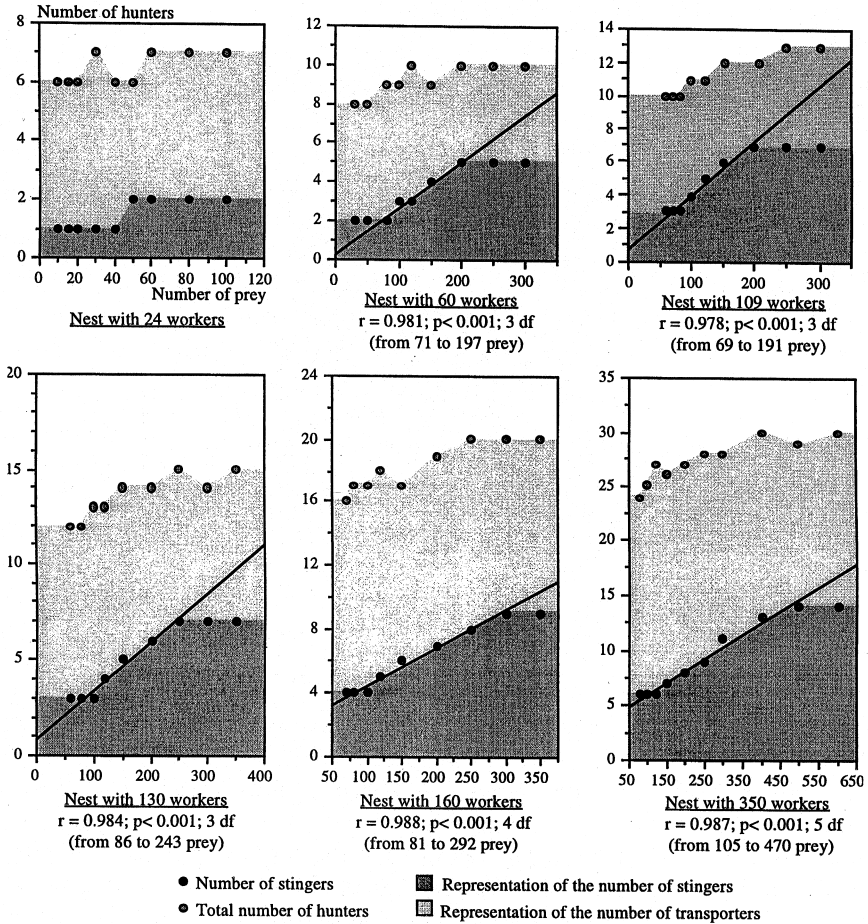


Fig. 3: Variations in the numbers of stingers and transporters according the quantity of prey supplied in the six other colonies. The correlation curves between the number of stingers and the quantity of prey supplied, and the corresponding minimal and maximal values of the number of stingers were calculated for each colony, except for the smallest one.

greater than the minimal one. The total number of hunting workers only increased by 13.9% (0% to 20%) between the minimal and the maximal values of stingers. Such a reduced increase in the total number of hunting workers cannot explain the marked increase in the number of stingers. Moreover, there was a significant positive correlation between colony size and the maximal value of the number of stingers ($r = 0.973; p < 0.001$). Simultaneously, the proportion of hunting workers in each behavioral subcaste was not significantly different among the seven colonies when the numbers of stingers reached their maximal values,

i.e. on average: 49.6% of hunting workers were stingers ($c^2 = 0.47$; n.s.) and 50.4% were transporters ($c^2 = 0.43$; n.s.).

Experiments 2 and 3: Determination of the "quantity of prey" by the hunting workers

Experiment 1 was used as a control. Only the surface of the hunting area was maintained constant while the number and density of prey were varied. The correlation curve between the number of stingers and the number, or the density, of prey was calculated (Fig. 1) allowing the expected number of stingers in the two other series of tests to be calculated. We considered that the "estimation of prey quantity" can be explained by an estimation of either the total number of prey (hypothesis 1) or the density of prey (hypothesis 2).

During experiment 2, the density of prey was kept constant (1.51 prey/cm²) while their quantity was varied (Fig. 4A). The expected number of stingers for the tested quantities of prey would be either variable from 3.28 to 10.82 individuals according the hypothesis 1 (variable number of prey) or constant at four individuals according to hypothesis 2 (constant density of prey). Our results showed that the number of stingers was equal to four individuals during the five tests.

Concurrently, experiment 3 was performed with a variable density of prey and a constant number of 400 prey (Fig. 4B). Here, the expected number of stingers for the tested densities of prey would be either constant at 11 individuals according to hypothesis 1 (constant number of prey) or variable from 3.63 to 10.54 individuals according to hypothesis 2 (variable density of prey). The observed number of stingers during the experiments was variable and very similar to the expected number of stingers according the hypothesis 2 (i.e. 4, 5, 7, 8 and 11 observed stingers vs. 3.63, 5.14, 7.30, 8.39 and 10.54 expected stingers, respectively, for the five tested densities of prey). Both results clearly indicate that prey density constitutes the triggering factor involved in the predatory response of *E. ruidum* hunting workers when faced with different quantities of prey.

DISCUSSION

Hunting workers of *Ectatomma ruidum* are able to estimate the "quantity" of prey at a given site according to an estimation of their density, and not according to their total number. Our experimental situation can be compared to the natural case encountered for the foragers of the formicine *Lasius niger*, which usually tends aphids. When homopteran aggregations are too important, the ant foragers prey on aphids and the quantity of captured individuals is correlated with

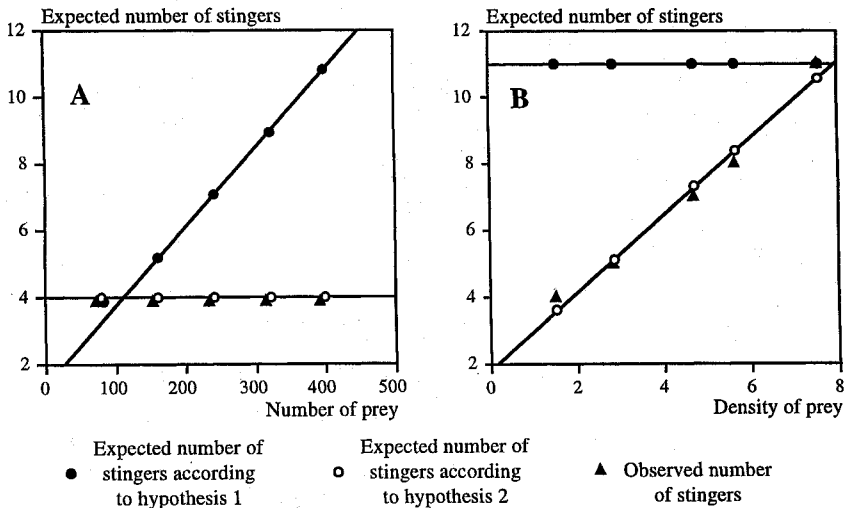


Fig. 4: Numbers of stingers observed during experiments and expected based on our hypothesis.

their density, and not with their total number (Sakata 1994, 1995). Such a process is likely to be involved in the variations in territory size in observed for the myrmicine *Solenopsis invicta* according to prey density (Showler *et al.* 1989) or the selection of the seeds of one plant species according to their density in granivorous ants (Johnson *et al.* 1994, also reviewed in Kunin 1994) and the strategy used to collect them (Bernstein 1975).

Two kinds of mechanisms could account for this capacity to estimate prey density: (1) either the hunting workers directly estimate the quantity of prey per "unit" of space or (2) they estimate, in an indirect way, the frequency of contact with prey per unit of time. In the first case, the hunting worker estimates the quantity of objects recognized as prey in its field of visual detection. It is generally accepted that the direct estimation of a quantity is hard for an invertebrate such as an ant, because it implies high-level cognitive abilities, such as the categorization and the abstraction of units to be quantified (Gelman & Gallistel 1978, Davis & Pérusse 1988). However, the ability to categorize is likely to exist in bumblebees (Dukas & Waser 1994) and in bees (Gould & Gould, 1988), and the ability to estimate a quantity put forth by Reznikova & Ryabko (1987, 1994) to explain observations performed during particular foraging situations in *Formica polyctena*. Nevertheless, Gordon *et al.* (1993) insisted on the necessity to involve the estimation of a more simple local element. This is why an estimation of the frequency of contact with prey seems more suited to estimate prey

density, because this hypothesis is more simply based on the estimation of temporal intervals between two contacts with prey. This second hypothesis is particularly conceivable in the case of *E. ruidum*, because the estimation of time duration and a relatively accurate use of the biological clock were clearly demonstrated in this species (Schatz *et al.* 1994, 1999b, Schatz 1997). The estimation of the density of a pertinent element of the environment via the frequency of contact with this element was recently proposed to explain the estimation of nestmate densities in *Lasius fuliginosus* (Gordon *et al.* 1993) and in *Linepithema humile* (Gordon 1995) thanks to simple models (Deneubourg & Franks 1995, Bonabeau *et al.* 1998).

Unlike *Pachycondyla caffraria* where stingers and transporters were also found (Agbogba & Howse 1992), the relative proportion of both of these behavioral subcastes remains stable when the number of stingers is minimal or maximal whatever the colony size, which suggests the existence of a highly flexible mechanism of social regulation among hunting workers (Schatz *et al.* 1996). Moreover, this stability was established with different proportions of stingers and transporters according to prey quantity: 49.6% and 50.4%, respectively, with a maximal number of stingers vs. 25.3% and 74.7% with a minimal number of stingers, these latter values being very similar to previous results (Schatz *et al.* 1996). As in other cases of social regulation (Lachaud & Fresneau 1987, Schatz *et al.* 1998a), the mechanism involved in our experiments may depend upon the competition for performing tasks based on a response threshold: the larger the number of prey killed in the hunting area, the fewer the opportunities for other hunting workers to act as stingers (Schatz *et al.* 1996, 1999a). Within a given range of variation, colonies of *E. ruidum* are then able to match the number of hunting workers specialized in stinging to the density of prey supplied. A similar ability exhibited during graded recruitment and the hunting strategies used by this species when confronted with large, heavy prey was demonstrated to be linked to three other characteristics: prey weight, prey size and the potential mortality risk due to prey defense (Schatz *et al.* 1997). Individuals are able to establish a kind of prey representation on the basis of these four characteristics (with perhaps others still unknown such as for *Anochaetus traegordhi*) (Schatz *et al.* 1999c), which is likely to explain individual improvements in the efficiency of prey capture observed in this species (Schatz, 1997) and also in other ponerine ants as, for example, such as *Pachycondyla villosa* and *Paltothyreus tarsatus* (Dejean *et al.* 1990, 1993).

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