

## Research article

# Raid process, activity pattern and influence of abiotic conditions in the slave-making ant *Rossomyrmex minuchae* (Hymenoptera, Formicidae)

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**Summary.** In the present work, we present the results of a study on the seasonal and daily activity, as well as on the raid process in *Rossomyrmex minuchae*. A comparative study of the annual and daily activity of the host species, *Proformica longiseta*, has also been made in parasitized and non-parasitized colonies. *R. minuchae* is an obligate slave-maker, in which the annual activity is strongly related to abiotic conditions, especially temperature and moisture of the soil. The raid process is comprised of three phases: scouting, assault of the host nest and robbing of the host brood. Recruitment of nestmates by mean of adult transport, concentration close to and invasion of the host nest, are the three tasks carried out by *R. minuchae* workers during the assault phase. Major differences between *Rossomyrmex* and *Polyergus* (the other obligate dulotic genus of the tribe Formicini) in terms of behaviour, both in nestmate recruitment and in the host-nest invasion, reflect different parasitic strategies in the two genera, supporting the assignment of these two genera to different phylogenetic groups.

**Key words:** Slave-making ants, Formicini, *Rossomyrmex minuchae*, *Proformica longiseta*, raiding and activity pattern.

## Introduction

Among the 8800 species of ants described (Hölldobler and Wilson, 1990), social parasitism is known in nearly 200 species of Formicidae. Of the parasitic species, 35 can be considered dulotic species (Buschinger et al., 1980), and belong to two subfamilies, Myrmicinae (Tribes Leptothoracini and Tetramoriini), and Formicinae (Tribe Formicini). Within the latter subfamily, three genera present dulosis: *Formica* (subgenus *Raptiformica* or *sanguinea* group, depending on the author), *Polyergus* and *Rossomyrmex*. Among these slave-makers, different degrees of specialization can be discerned; thus, among the species of the genus *Formica*, belonging to the group *sanguinea*, the taking of booty is facultative

(Wilson, 1971; Hölldobler and Wilson, 1990), while in *Polyergus* and *Rossomyrmex proformicarum*, the slaves are indispensable to the maintenance of the colony (Marikovsky, 1974; Topoff et al., 1985b; Hölldobler and Wilson, 1990; Le Moli et al., 1994; Hasegawa and Yamaguchi, 1994). Most studies on parasitic Formicini present ecological and behavioural data on *Polyergus* species: *P. rufescens* in Europe (Czechowski, 1975; Mori et al., 1991; Le Moli et al., 1994), *P. lucidus* (Talbot, 1967; Kwait and Topoff, 1984) and *P. breviceps* (Topoff et al., 1985a and b) in North America and *P. samurai* (Hasegawa and Yamaguchi, 1994, 1995) in Japan. Traditionally, the genera *Polyergus* and *Rossomyrmex* have been considered phylogenetically close (Wilson, 1971; Buschinger, 1990; Hölldobler and Wilson, 1990; Agosti, 1989; Agosti, 1994), thus implying a monophyletic origin of parasitism in Formicini.

*Rossomyrmex minuchae* Tinaut, 1981, together with *Rossomyrmex proformicarum* Arnoldi, 1928 are the only two species belonging to the genus *Rossomyrmex* Arnoldi, 1928. Works published on the biology of this genus up to now include only data on *R. proformicarum* (Arnoldi 1928, 1932, Marikovsky 1974).

*R. proformicarum* is distributed throughout the plains of the Caspian Sea (Russia) and the foothills of Tian-Shan (Kazakstan) (Arnoldi 1928, 1932, Marikovsky 1974), while *R. minuchae* appears only in extremely localized zones of the cold-xeric steppe of the Sierra Nevada Mountains (southern Spain) (Tinaut, 1981; Tinaut et al. 1994).

*R. minuchae* was described from only one nest (Tinaut, 1981), and afterwards, despite intense studies on the zone and the host species (Tinaut 1979, 1981; Fernández et al., 1993; Tinaut and Fernández, 1993; Fernández and Tinaut, 1998), no more than 20 nests have been discovered in this species. The finding of these nests since 1990 allowed us to undertake the study of the biology, ecology and behaviour of *R. minuchae*. In this first report, we present details concerning the annual and daily activity of this species, abiotic conditions involved, and the raid process. Other biological and

ethological aspects have been studied and shall be examined further in forthcoming papers.

## Materials and methods

### Natural history of the host

*Proformica longiseta*, the host species of *R. minuchae*, is endemic in the high mountain of the southeastern Iberian Peninsula (Sierra Nevada, Sierra de los Filabres and Sierra de Gádor). The distribution of *P. longiseta* is between 1800 and 2700 m a. s. l., both in limestone and siliceous soils, but invariably in the most arid biotopes (Tinaut, 1979). The nests remain under snow for 5 or 6 months per year. This species is monomorphic and allometric and has a subcaste of repletes (Fernández et al., 1994). The ant nests are monodomic and predominantly polygynic.

### Abiotic conditions

The abiotic conditions measured were: at = air temperature at 1 m above ground; st = soil temperature at 0.5 cm beneath surface; ah = air humidity at 1 m above the ground; sm = soil moisture at 0.5 cm beneath surface. These variables were measured hourly from 10 to 21 h, every 15 days from the end of May until the beginning of September, and daily for the duration of the *R. minuchae*'s daily activity. A Rotronic-Hygroskop GT thermometer-hygrometer (Rotronic AG Switzerland) was used for measures. The abiotic conditions measured were those that most influence the activity of *P. longiseta* (Fernández and Tinaut, 1998).

### Activity pattern

The methodology followed to study the activity during the summer of 1995 consisted of hourly 10-min observations from 10 to 21 h (local time), of 2 non-parasitized nests and 3 parasitized nests, counting the entries and exits of all the workers, regardless of the species. This sampling was conducted every 15 days from the end of May until the beginning of September, the active period of the host. With these data, we calculated means of daily activity (entries + exits/10 minutes each hour) and annual activity (mean of active workers each sampling day) for the *P. longiseta* workers (of parasitized and non-parasitized nests) and *R. minuchae*. In addition, from the daily observations of 5 *R. minuchae* nests (see section on the raid process), we also calculated the maximum frequency of nests showing *R. minuchae* activity each day. These results were pooled to obtain a 5-day mean, in order to gain a more general view of the annual activity of *R. minuchae*, due to the irregularity in daily activity in the *R. minuchae* nests.

### Ant-nest populations

Nine *Rossomyrmex minuchae* and 29 *Proformica longiseta* ant nests were unearthed during the 7 study years. The entire population was collected and counted in the laboratory.

### Raid process

Five *R. minuchae* nests were visited daily over the summer of 1995. The observation time was 10 min per hour from 10 to 21 h (local time) from the first sighting of an active *R. minuchae* (21 June) until the nest activity ceased (3 August), and notes were taken concerning the type of activity in each nest. In addition, during these observations, we followed the worker scouts over the ground, recording the type of activity, distance travelled, the trajectory followed leaving and returning to the nest, and whether or not they located a host nest. When they located a host nest, we recorded the sequence of events – that is, recruitment, number

of workers participating in the raid, and, overall, how the raid was accomplished. For each raid, the timing of each activity, the duration of daily activity and duration of the entire raid were recorded.

### Statistical treatment

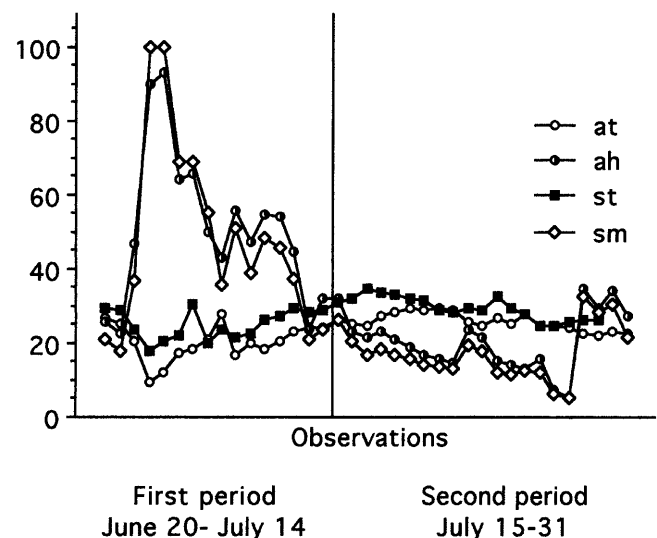
Using a Mann Whitney U-test (Sokal and Rohlf, 1995), we compared the daily means of the different abiotic factor measured according to the active period, and similar comparisons were made for the daily activity and the percentage of active *R. minuchae* nests.

A linear regression (Sokal and Rohlf, 1995) was performed between the means of each of the 4 abiotic variables measured, and the means of the seasonal activity of each species, as well as of the maximum frequency of the active *R. minuchae* nests. A curvilinear (quadratic) regression (Sokal and Rohlf, 1995) was fitted to data from the means of the daily activity of each species related to daily means of the soil temperature. To test whether the abiotic factors measured influenced the seasonal and daily activity of the two species, we obtained the Pearson R<sup>2</sup> Coefficient (Sokal and Rohlf, 1995).

## Results

### Abiotic conditions in the study zone

During the sampling season of *R. minuchae* activity, two periods were distinguishable (Fig. 1). The first period, from 20 June to 14 July, was characterized by strong fluctuations in the abiotic conditions, especially in air humidity and soil moisture. In this period of time, rain and clouds were frequent, and thus the daily means of the air humidity and soil moisture proved higher (ah mean = 33.6; sm mean = 42.3), causing great fluctuations (ah range = 22.7 to 93%, sm range = 18.1 to 100%), whereas the mean air temperature was below 25°C (mean = 21.2°C; SE = 0.9; n = 22), and



**Figure 1.** Means for daily environmental conditions in the study zone during the first (from 20 June to 14 July) and second period (from 15 July to beginning of August) (at = air temperature at 1 m from the ground; ah = air humidity at 1 m from the ground; st = soil temperature at 0.5 cm beneath the soil; sm = soil moisture)

the mean soil temperature below 30°C (mean = 25.2°C, SE = 0.8; n = 20). The second period, from 15 to 31 July, showed more stable abiotic conditions. The daily means of air humidity (ah mean = 18.1%; SE = 1.0; n = 13) and of soil moisture (sh mean = 15%; SE = 0.7; n = 13) decreased consistently to below 25% (ah range = 13 to 24%; sm range = 11.5 to 19.7%) while mean temperatures of air (at mean = 27.3°C; SE = 0.5; n = 13) and of the soil (st mean = 31.3°C; SE = 0.5; n = 13) rose during this period, narrowing their variation range (at range = 25.0 to 29.6°C; st range = 28.5 to 34.6°C). Significant statistical differences appeared between the two periods in the means of central trend with respect to air temperature (Mann Whitney U-test,  $p < 0.0001$ ), soil temperature ( $p < 0.0001$ ), air humidity ( $p < 0.0001$ ) and soil moisture ( $p < 0.0001$ ).

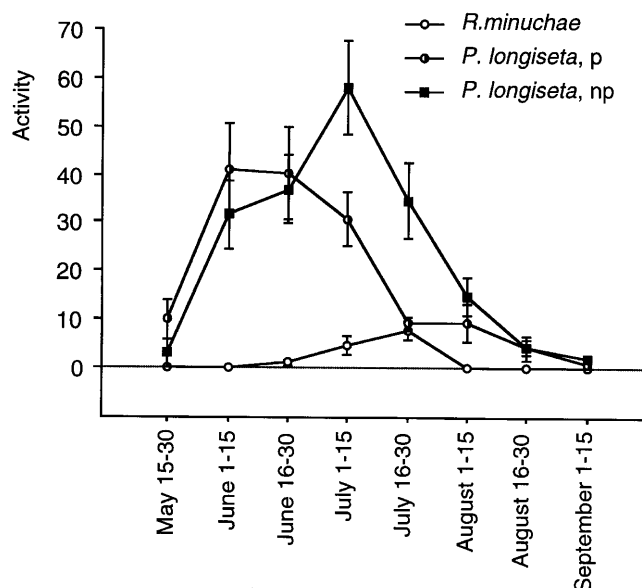
### Annual activity

The host species, *P. longiseta*, in the non-parasitized ant nests, began its annual activity in the study zone in last-May, reaching its highest activity in the first fortnight of July (Fig. 2). Afterwards, activity began to decline, reaching the lowest levels towards the last fortnight in August. Parasitized nests registered their highest activity during June, with an abrupt decline in the first fortnight of July, thereafter remaining at the lowest levels.

*R. minuchae* workers were never seen seeking food on the exterior nor transporting any prey which were not the product of a raid. In no case were *R. minuchae* workers seen defending their nest. Parasitized ant nests usually presented *R. minuchae* activity from the last ten days of June to the first few days of August (Fig. 2). The highest number of active workers was registered from 16 to 30 of July. Annual activity fell rapidly between the last days in July and the first few days of August, when the parasite completely disappeared. Even in the most active nests, parasite presence on the outside was not continuous, but rather periods of constant activity lasting up to 6 consecutive days alternated with inactive periods of up to 5 days. The parasitized nests presented *R. minuchae* activity an average of 13.2 days (range = 10 to 16; n = 5 nests) in the summer of 1995.

No statistical correlation was found between the mean number of active *R. minuchae* workers and the environmental factors studied. *R. minuchae* workers were active within broad ranges of variation of abiotic factors. The only factor which decisively inhibited worker activity was heavy moisture – workers were never active when ah exceeded 66% or when sm was greater than 70.3%. Regarding temperature, worker activity continued at air temperatures between 16.5 and 38.7°C, and at soil temperatures between 19.1 and 40°C, activity ceasing over these maximum temperatures.

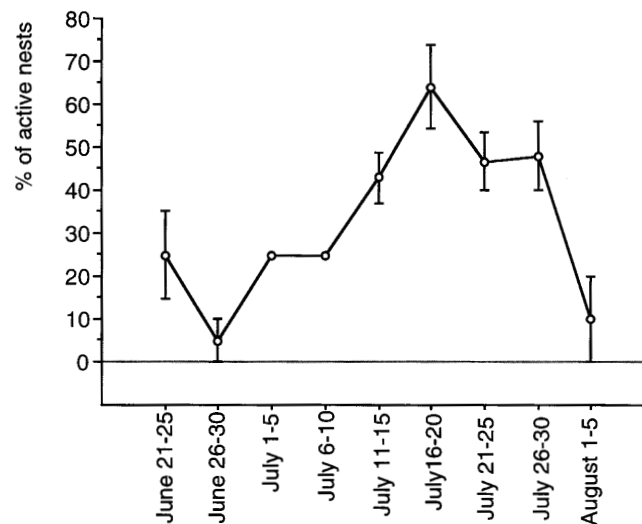
The mean percentage of parasitized nests with *R. minuchae* activity fluctuated over the season, with the highest values recorded in the second fortnight of July (Fig. 3). The greatest percentage of active ant nests (80%) was recorded on 6 days (14.3% of the period of total activity), between 15 and 27 July. The mean percentage of nests with *R. minuchae*



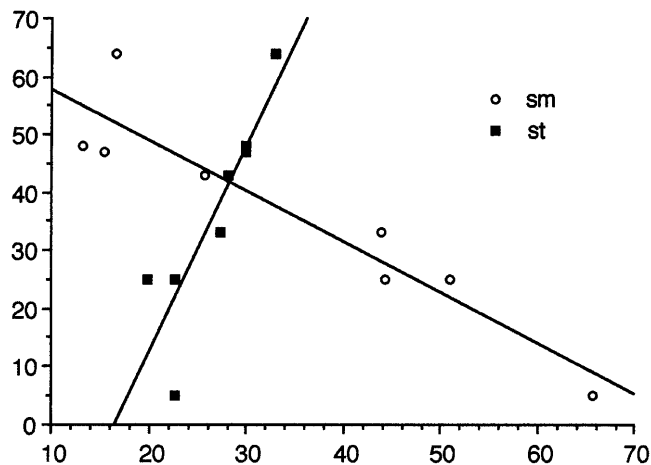
**Figure 2.** Annual fluctuation of activity (average number of entries and exits/10 min/h) of parasitized (p) and non-parasitized (np) *P. longiseta* and *R. minuchae*. Mean and standard error (SE) were obtained from each fortnight sampling

activity differed significantly between the first and second period, as occurred with the abiotic conditions (Mann Whitney U-test,  $p = 0.003$ ), doubling the probability of finding nests with *R. minuchae* activity in the second period.

The mean percentage of active *R. minuchae* nests every 5 days correlated positively with mean temperature and negatively with mean relative humidity, and was highly influenced by abiotic soil factors; especially soil moisture explained the highest amount of the variation in the percentage of nests with *R. minuchae* activity (Fig. 4; st:  $R^2 = 0.766$ ,  $p = 0.0044$ ; sm:  $R^2 = 0.876$ ,  $p = 0.0006$ ), although the interpretation of



**Figure 3.** Percentage of nests with *R. minuchae* activity each 5 days of the sampling season. Mean and standard error (SE) are given



**Figure 4.** Linear regression between the mean values of soil moisture ( $sm = X_1$ ) and soil temperature ( $st = X_2$ ), and the mean percentage of nests with *R. minuchae* activity ( $Y$ ). ( $Y_1 = 66.4 - 0.8 X_1$ ;  $R^2 = 0.87$ .  $Y_2 = -57.3 + 3.5 X_2$ ;  $R^2 = 0.76$ )

the relative importance of temperature versus moisture was made difficult by the strong dependence of the two.

#### Daily activity

With respect to the fluctuation of the abiotic factors during the day (Fig. 5a), we found that the air and soil temperatures rose over the day, peaking at 16 h (at mean = 25.8°C; st mean = 37.8°C), and st remained above 30°C from 13 to 19 h. The ah and sm began to fall sharply after 13 h, reaching the lowest levels at 17 h (ah = 26%; sm = 20.4%).

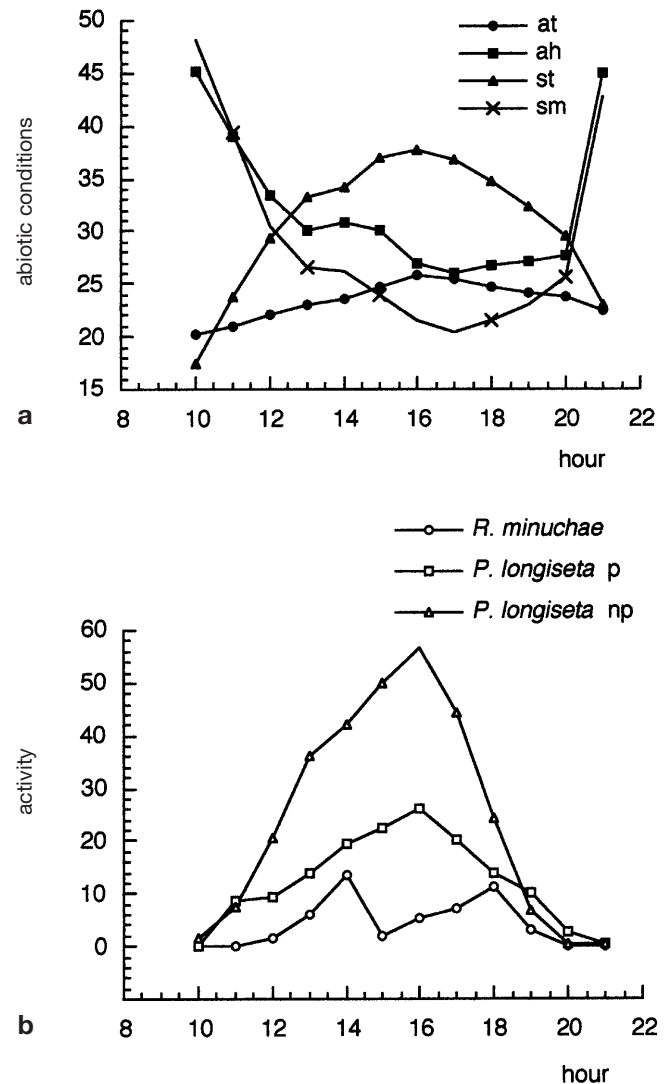
In the parasitized nests, *R. minuchae*, when active outside the nest, appeared between 12 and 20 h (Fig. 5b). This was a bimodal cycle, with a dip in activity at 15–16 h and two peaks, one at 14 h and the other at 18 h.

*P. longiseta* nests showed a unimodal daily activity cycle, with a peak at 16 h (Fig. 5b). In addition, the activity in parasitized nests proved lower than in non-parasitized nests, but with the same activity pattern.

By quadratic regression, we sought to identify which daily pattern of activity was more strongly related to abiotic factors. The amount of variation in daily activity explained by abiotic factors, especially by soil temperature (Fig. 6), was higher in *P. longiseta*, both in parasitized and non-parasitized nests ( $R^2 = 0.84$ ;  $R^2 = 0.8$ ), than in *R. minuchae* ( $R^2 = 0.55$ ). *P. longiseta* tended to increase its daily activity with higher soil temperatures while *R. minuchae* decreased its activity at 35°C and higher (Fig. 6).

#### Ant-nest population

The average number of *P. longiseta* workers in the parasitized nests was greater (mean = 650.7; SE = 212.5) than in the non-parasitized nests (mean = 497; SE = 48.9), although the parasitized nests showed a much higher variation in the

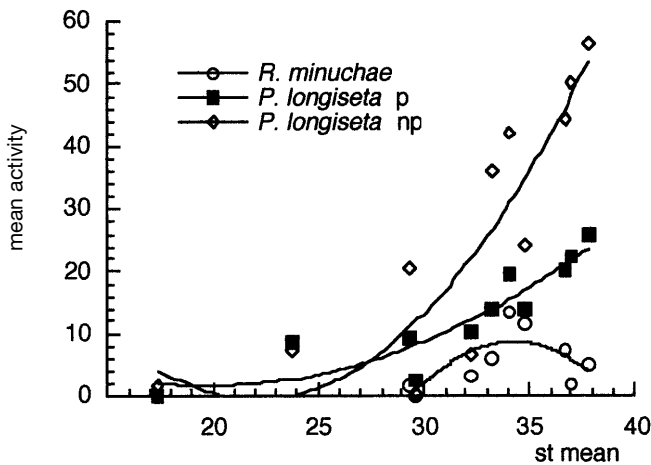


**Figure 5.** Daily fluctuation in: a) environmental conditions and b) activity of *P. longiseta* parasitized (p) and non-parasitized (np) and *R. minuchae*. The points on the graph are mean values of all the observation days

number of *P. longiseta* workers. In the 9 parasitized nests which we unearthed, we consistently found the two species together. The host:parasite ratio was around 5 *P. longiseta*:*R. minuchae*, with a mean of *R. minuchae* population of 122.5 workers (SE = 16.7).

#### Raid process

The raid process of *R. minuchae* consists of three activities, which were the only activities for which the workers of this species left their nest (excluding help to reproductive caste, which will be reported in a forthcoming manuscript): scouting (the search for host nests), assault (attack of the host nest) and brood robbing (carrying away of host brood). There is a logical sequence in the three tasks which *R. minuchae* workers pursue outside the nest.



**Figure 6.** Quadratic regression between the mean soil-temperature measurements (st) for each hour (X), as well as the mean activity per hour of: *R. minuchae* ( $Y_1$ ) and *P. longiseta* parasitized (p) and non-parasitized (np) ( $Y_2$  and  $Y_3$  respectively). ( $Y_1 = -420.2 + 25 X - 0.365 X^2$ ;  $R^2 = 0.55$ .  $Y_2 = 27.9 - 2.7 X + 0.06 X^2$ ;  $R^2 = 0.84$ .  $Y_3 = 106.4 X - 9.7 X + 0.22 X^2$ ;  $R^2 = 0.8$ )

The scout phase is the first, between 12 and 19 h (local time). Scouting activity slows at 15 h, and reaches a peak at around 17 h. The duration of this phase is extremely variable, from 2 h to 7 days – depending on the time needed to find a host nest. The abiotic conditions under which this activity occurs also cover a rather broad range: (at: 19.1 to 38.7°C; st: 23.1 to 40°C; ah = 8.2 to 49.1%; sm = 5.3 to 44.5%). In general, scouting represents 42% of the total activity time of *R. minuchae* in each nest (SE = 5.25; n = 5; range = 28 to 52%). The 5 nests studied during 1995 engaged in scouting a total of 87 times with a mean of 10.7 workers/10 min (SE = 1.2; n = 87). A total of 17 *R. minuchae* workers were followed during the scouting phase; these scouts combed a sector near the home nest and ventured an average of 3 m away (SE = 0.4; range = 0.3 to 6.2 m). Independently of the distance travelled, the exploration mechanism of a scout has a rather set pattern. Firstly, the direction taken is quite linear, and, at the end of this trajectory, the true exploration begins, as the scout enters all holes encountered, and leaves with erratic changes in directions. Whether or not a host nest is found, the scout returns to the home nest, although the return is swifter after a host nest is located.

The scout that discovers a host-nest location begins the assault against the *P. longiseta* nest selected. The first stage of the assault is the recruitment of nestmates: the scout returns to the home nest and causes excitation among nestmates. Outside and at the entry of the nest, the scout uses its mandibles to seize a nestmate and carry it to the target nest. The worker being transported adopts the classical position of adult transport described for Formicini (Arnoldi, 1932; Möglich and Hölldobler, 1974; Hölldobler and Wilson, 1990). Both the recruiter scout and the recruited worker return to the home nest and each transports a nestmate back to the target nest, and thus the number of recruits grows in a roughly geometric progression. The total number of workers

that participate in the raid reaches between 60 and 90. At a certain moment, the chain of recruitment is broken and all of the workers involved amass not far from the target nest. This concentration, the second stage of the assault, ends with the invasion of the target nest, the third and final stage. We have witnessed 18 assaults, which usually begin around 17 and 19 h. The temperature range at the moment of the assault is approximately the same as that of scouting, though slightly more restricted (at = 20.1 to 30.5°C; st = 24.6 to 35.8°C; ah = 12.6 to 49.2%; sm = 10.4 to 37.8%). The assault process occupied an average of 18% of the total activity time of *R. minuchae* workers (SE = 2.92; range = 7 to 23; n = 18). Most of the nests assaulted during the study period (65%) were situated at 3 to 5 m from the parasitic nest.

During the activity period of 1995, each of the 5 *R. minuchae* nests launched assaults on 2 to 5 host nests (mean = 3.6; SE = 0.6). The percentage of failures – that is, assaults which did not succeed in robbing brood – was 40% (7/18). In most of these unsuccessful raids (70%; 5/7), not even the recruitment phase was finalized, while in only 30% (2/7) the raid failed after the invasion of the host nest. The successful assaults lasted some 90 min (mean = 99; SE = 13.6; range = 52 to 135; n = 6). During the invasion, some parasitic workers dug into the nest to reach shallow chambers while others invaded directly through the main entrance of the nest. No strong signs of aggression were evident outside the nest, although it was common to see two or three *P. longiseta* workers fighting against a *R. minuchae* worker and one or two *P. longiseta* workers trying desperately to close the entrance of the nest. Internally, the struggle must be greater, since sometimes *P. longiseta* workers and the queen or queens left the nest, searching for a new hole for refuge. In addition, during the robbing of the brood, only a few smaller *P. longiseta* are transported alive, while most other workers are taken away dismembered. However, *R. minuchae* do not appear to suffer casualties. At the end of the assault, some *R. minuchae* returned to the home nest without taking prey but the most remained inside the assaulted nests.

The robbing of the brood does not begin until the second day, almost exactly 24 h after the recruitment began. The parasitic workers leave the target nest not only with *P. longiseta* pupae, but also with larvae, eggs, small live workers, worker remains and especially the gasters of dismembered replete workers. This is the most extended and uninterrupted activity of the day, usually beginning at about 17 h of the day after the raid, and commonly lasting for more than one day, from 12 to 20 h, with a short lag around 15 h. An average of 18 *R. minuchae*/10 min (SE = 2.0; n = 69) remained active in the target nest.

Brood robbing occupied 40% of the total *R. minuchae* activity time outside the parasite nest (SE = 7.11; n = 5; range 28.6 to 65%). Among the 11 successful assaults perpetrated during 1995 by the 5 *R. minuchae* nests, we recorded brood robbing 10 times and in one other case the result of the raid was the nest relocation of the entire parasitic nest, including the slaves, the parasite brood and the parasite queen, instead of the expected robbing of the brood. During the summer of 1995, the *R. minuchae* nests robbed the brood of between

1 and 3 host nests (mean = 2.2; SE = 0.37; n = 5), the average duration of these raids being 2 days (mean = 2.2; SE = 0.33; n = 10; range = 1 to 4 days).

## Discussion

Data for *R. proformicarum* and *R. minuchae* could be compared only loosely because the data for *R. proformicarum* were less detailed, although the behaviour of the two species is similar in general terms.

*R. minuchae* is an obligate parasite species, in which the workers pursue no activity outside the nest other than raids. On the contrary, *R. proformicarum*, also an obligate parasite, emerges on the exterior to defend its nest (Marikovsky, 1974).

The duration of the annual period of activity in *R. minuchae* is slightly shorter than that of *P. samurai* (Hasegawa and Yamaguchi, 1994) and *P. lucidus* (Talbot, 1967). The abiotic conditions, especially of the soil, have a strong relationship with the annual activity of *R. minuchae*, as in *Polyergus* (Mori et al., 1991; Hasegawa and Yamaguchi, 1994); thus the number of active *R. minuchae* nests doubled when average soil temperatures were high and the average relative moisture was low. On the other hand, the seasonal activity of *R. minuchae* cannot be considered to be related to brood availability in host nests (Buschinger et al. 1980), as reported for *P. samurai* (Hasegawa and Yamaguchi, 1994) and *P. lucidus* (Talbot, 1967), given that *P. longiseta* queens are capable of laying eggs immediately after coming out of hibernation (May), as an adaptation to the brief vegetative period (Fernández-Escudero et al., 1997), and the presence of larvae or pupae persists from the beginning of June until the end of July.

In its daily activity, however, *R. minuchae* remains inactive between 15 and 16h, the hottest period, resuming their activity during a broader time span than does *Polyergus*, which becomes active only in the afternoon (Talbot, 1967; Topoff et al., 1985a; Mori et al., 1991; Hasegawa and Yamaguchi, 1994). Another particularity is that the parasitized nests do not reveal *R. minuchae* activity every day, whereas the *Polyergus* nests show daily activity, at least in the scouts (Le Moli et al., 1994).

*R. minuchae* launches its raids on climatologically stable and sunny days, as in the *Polyergus* species (Mori et al., 1991; Hasegawa and Yamaguchi, 1994). The mean soil temperatures at which both species carry out raids are similar, around 30°C (Mori et al., 1991; Hasegawa and Yamaguchi, 1994; Le Moli et al., 1994). *R. minuchae* can remain active over a wider range of temperatures, reaching 40°C, but does not conduct raids when the relative humidity exceeds 50%. In contrast, *Polyergus* does not tolerate temperatures above 32°C (Hasegawa and Yamaguchi, 1994; Topoff et al., 1985), and makes raids only when relative humidity is high, over 60% (Mori et al., 1991; Hasegawa and Yamaguchi, 1994; Le Moli et al., 1994). The abiotic preferences of *R. minuchae*, like those of *R. proformicarum* (Marikovsky, 1974) and *P. longiseta* (Tinaut and Fernández, 1993), are consistent with the typically steppe distribution of both genera (Arnoldi,

1932; Marikovsky, 1974; Tinaut, 1979). *Polyergus*, however, prefers less-arid environments, and in desertic habitats, occupies microhabitats near water courses having riparian vegetation (Topoff et al., 1985a).

*R. minuchae* can remain active over a wide range of abiotic conditions, especially when carrying out tasks of little risk to the colony. High-risk tasks, such as the assault, which involves a high number of workers during a brief period of time, is performed under more specific abiotic conditions. Both scouting and the assault are undertaken under similar environmental conditions, while brood robbing encompasses the entire day, almost regardless of abiotic conditions, except relative humidity. This indifference is probably because this activity is highly beneficial to the colony and once under way carries little risk even for the individual carrying the booty, given that the predators prefer mainly larvae, pupae and especially gasters of replete workers, transported by the workers of *R. minuchae*.

The mid-afternoon hours of *R. minuchae* inactivity coincide with the time of greatest activity of *P. longiseta*, and, although this might be the best period for the parasite to locate host nests, it would also be the most propitious time for the host to detect the intended assault and eliminate the element of surprise, thereby probably increasing the conflict between the parasite and host (Tinaut and Ruano, 1998).

While the pattern of activity among *P. longiseta* workers from parasitized nests parallels that of *P. longiseta* from non-parasitized nests, two peculiarities emerge. Firstly, the daily number of *P. longiseta* workers active outside was lower in parasitized than in non-parasitized nests despite that parasitized nests contained a greater mean number of workers than did non-parasitized nests. Secondly, the slaves registered an extraordinary descent in seasonal activity as the activity of *R. minuchae* reached its yearly maximum. Both of these features appear to be attributable to the greater amount of work to be done by the slaves inside the parasitized nest. This seasonal change, having no parallel in non-parasitized nests, cannot be explained by a decline in resource availability or change in abiotic conditions.

The close relationship between decreased *P. longiseta* activity and increased *R. minuchae* activity appears to be due to two intertwined factors. That is, over the season, as the number of foraging slaves, and thus the food supply, diminish, *R. minuchae* may be forced to increase its activity in search of new resources. In turn, as new slave brood and additional food are brought into the nest, *P. longiseta* are needed more inside the nest than outside.

Another major peculiarity of *R. minuchae* is the low average number of raids per season (3.6 raids/parasitic nest/year vs between 19 and 63 raids/parasitic nest/year in *Polyergus*; Talbot, 1967; Hasegawa and Yamaguchi, 1994; Le Moli et al., 1994). This difference may be related to the massive host-nest exploitation by *R. minuchae*, and the duration of various days of brood robbing, after which the host nest is completely devastated. Only occasionally does a small part of the population manage to escape and occupy a new hole nearby, but these new nests are usually detected in the same year or the following one. According to the mean population of parasit-

ized and non-parasitized *P. longiseta* nests, it is evident that two or three raids provides an adequate supply of slaves for a *R. minuchae* nest.

The raid strategy of *R. minuchae*, in which a struggle is evident within the host nest, also differs with respect to *Polyergus*. The latter species provokes the secretion of an alarm pheromone in *Formica*, which then abandon the nest (Topoff, 1990), allowing the parasite to plunder of the pupae without resistance (Topoff, 1990; Hasegawa and Yamaguchi, 1994; Talbot, 1967; Le Moli et al., 1994). In addition, the recruitment method differs in the two dulotic Formicinae: *Polyergus* uses recruitment by pheromones (Talbot, 1967; Hasegawa and Yamaguchi, 1994; Le Moli et al., 1994), while *Rossomyrmex* recruitment takes the form of adult transport. This is the only dulotic genus that uses this method of recruitment to the host nest (Arnoldi, 1932; Tinaut and Ruano, 1998). In the non-parasitic genera (i.e., *Formica* or *Myrmica* among others) the recruitment by adult transport is used only for nest relocation (Wilson, 1971; Hölldobler and Wilson, 1990).

Therefore, these basic differences between *Rossomyrmex* and *Polyergus* in preferences regarding abiotic conditions, nestmate recruitment and host-nest raiding indicate that the two genera use different strategies and undoubtedly have different phylogenetic origins (Tinaut et al., 1994; Hasegawa et al., in prep.). Finally, this implies a polyphyletic origin of parasitism within Formicini.

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