Foraging Activity and Dietary Spectrum of the Argentine Ant (Hymenoptera: Formicidae) in Invaded Natural Areas of the Northeast Iberian Peninsula

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ABSTRACT We analyzed the foraging activity and the dietary spectrum of the Argentine ant (*Linepithema humile* Mayr) and select native ants on cork oaks from Mediterranean open cork oak (*Quercus suber*) secondary forests. The study areas included invaded and noninvaded zones in close proximity. The Argentine ant's daily foraging activity was correlated to the abiotic factors studied, whereas the seasonal foraging activity was related not only to the variations in the average air temperature, but also to the trophic needs of the colony. Argentine ant workers focused their attention on protein foods during the queens' oviposition periods and during the larvae development phase, and on carbohydrate foods, such as honeydew, when males and workers were hatching. There were no significant differences over the entire year in the quantity of liquid food collected by the Argentine ant workers in comparison with the native ants studied. The solid diet of the Argentine ant on cork oaks is composed of insects, most of which are aphids. Our results have clear applications for control methods based on toxic baits in the invaded natural ecosystems of the Iberian Peninsula.

KEY WORDS Argentine ant, dietary spectrum, foraging activity, *Linepithema humile*, *Quercus suber*

The Argentine ant (*Linepithema humile* Mayr) is a widespread invader (see http://www.issg.org/database). Native to South America, it has been introduced worldwide because of human commercial activities (Hölldobler and Wilson 1990, Suarez et al. 2001). Its distribution range includes areas with Mediterranean-type climates throughout the world (Passera 1994, Suarez et al. 1998). In the Iberian Peninsula, it is spread out extensively over the entire coastal band (Espadaler and Gómez 2003). Although the Argentine ant is associated with human-altered habitats (Suarez et al. 1998), there is increasing evidence of its ability to colonize natural areas with low anthropogenic disturbance (Cole et al. 1992, Human and Gordon 1996, Holway 1998a, Suarez et al. 2001, Gómez et al. 2003). It is widely reported that, in these areas, the Argentine ant affects the native fauna, leading to changes in some essential ecological processes such as seed dispersal (Bond and Slingsby 1984, Gómez and Oliveras 2003) and pollination (Visser et al. 1996, Blancafort and Gómez 2005), therefore having a negative impact on native biodiversity. The Argentine ant also produces negative economic effects by invading crops and plantations because of its mutualistic interactions with hemipterans, which can affect the growth and production of the host plant (Buckley 1987, Ness and Bronstein 2004).

Attempts at eradicating established populations of Argentine ants have had little success. Current control methods focus on using toxic baits (Baker et al. 1985, Krushelnycky and Reimer 1998a, b, Silverman and Roulston 2001, Klotz et al. 2004). However, the success of this method depends on various factors including the attractiveness of the food for the foraging ants. Therefore, studies on the seasonal food preferences of the Argentine ant and its foraging activity periods are essential for effective use of toxic baits. To date, the most complete study on the foraging and feeding behavior of *L. humile* was done by Markin (1970a) in a California citrus grove, but only a few studies present any data about the food preferences of this species in an invaded natural area (Human et al. 1998, Zee and Holway 2006).

The purpose of this paper is to examine the foraging activity times and the dietary spectrum of the Argentine ant in cork oaks of a natural ecosystem. This is a preliminary and indispensable step toward providing valuable information that can be used to develop control methods based on using baits in Mediterranean invaded natural ecosystems.

Materials and Methods

Study Area and Plant Species. This study was carried out in open cork oak secondary forests dominated by *Quercus suber*, *Quercus ilex*, *Erica arborea*, *Cistus monspeliensis*, *Cistus salvifolius*, and *Arbutus unedo* on the

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southern edge of the Gavarres Massif, near the village of Castell d'Aro (Northeast Iberian Peninsula; 41°49′ N, 3°00′ E). The study areas are 4 km from the Mediterranean coast. This region has a Mediterranean subhumid climate, with 750–800 mm annual rainfall. In these areas, there are invaded and noninvaded zones in close proximity (≈1.5 km apart) with similar environmental characteristics. The cork oak (*Quercus suber* L.) was chosen to study the foraging activity and dietary spectrum of the Argentine ant because it is the main tree species in the study areas and also because it allowed us to study both the liquid and solid diet of this ant.

The exploitation of liquid sources in *Q. suber* throughout the year was studied to analyze how liquid food sources are used by the Argentine ant. In addition, we also studied the native ants that collect liquid food sources from *Q. suber* to compare their behavior with that of the Argentine ant.

Argentine Ant's Daily Foraging Activity on Cork Oaks. We selected at random five cork oaks from the invaded zones and five more from the noninvaded ones. They were at least 10 m apart. In all cases, the ants were nesting in the trees themselves (near the roots). Foraging activity was determined by counting the number of ants moving up and down the tree trunk for 5 min every hour during the sampling day.

To determine if a daily pattern existed in the Argentine ant's foraging activity, sampling was carried out each hour over a 24-h period each month from May to September 2004 (warm period) and from December 2004 to January 2005 (cold period). The air temperature and the relative humidity for each sampling hour were also registered.

The correlation between the daily foraging activity and the abiotic factors studied was evaluated for each sampling day to assess whether the daily foraging activity and these factors were connected. Correlations were measured with Pearson's correlation coefficient.

Differences between the diurnal foraging activity (from 0900 to 2000 hours) and the nocturnal foraging activity (from 2100 to 0800 hours) of all the sampling days corresponding to the warm period were compared using a one-factor repeated measures analysis of variance (ANOVA).

Seasonal Foraging Activity on Cork Oaks. We estimated the seasonal foraging pattern of the Argentine ant from 0900 to 2100 hours, 1 d/mo during 2004 and every 15 d during 2005/2006. The air temperature and the relative humidity for each sampling hour were also registered.

The seasonal foraging pattern in cork oaks was also measured for the native ant community to evaluate possible differences between this community and the Argentine ant. In this case, sampling was carried out from 0900 to 2100 1 d/mo during a 2-yr period (2004–2006).

The correlation between the seasonal foraging activity and the average air temperature and humidity registered during the sampling hours was measured.

Liquid Food Collection from Cork Oaks. The daily amount of liquid food collected by the ants was measured by capturing 20 ants going up the tree (without liquid) and 20 ants going down the tree (with their gasters full of liquid) every 2 h during the sampling day. The captured ants were frozen to avoid losing liquid until they were weighed with a precision balance ($\pm 10^{-4}$ g) in the laboratory. The average difference between the weight of the ants with liquid and the weight of the ants without it was taken as an estimator of the amount of liquid food collected by 20 workers. The average amount of liquid food transported by a single worker was estimated. This value, multiplied by the estimated foraging activity of the whole sampling day, was used to estimate the daily amount of liquid food collected by the ants.

Solid Prey Captured by the Argentine Ant on Cork Oaks. Every 2 h for 5 min, we counted the ants that returned to the nest with visible prey between their mandibles and the total number of ants that entered the nest during this period. We calculated the proportion of ants that returned to the nest with solid prey between their mandibles in relation to the total number of ants coming back to the nest. Samples were taken from 0900 to 2100 hours on the same sampling days as for the Argentine ant's seasonal foraging activity observations. The solid prey captured by the Argentine ants was also collected and taxonomically classified in the laboratory.

All statistical analyses were run under the SPSS statistical package for Windows version 12.0.1 (SPSS, Chicago, IL).

Results

Argentine Ant's Daily Foraging Activity on Cork Oaks. The Argentine ant's daily foraging activity on cork oaks was continuous throughout the day and night during the warmer months (May to September; Fig. 1). During this period, nocturnal foraging activity was significantly higher than diurnal foraging activity ($F_{1,299} = 114.351$, $P < 0.001$).

The diurnal foraging activity pattern was negatively correlated with the air temperature and positively correlated with humidity for all 5 mo sampled (Pearson's correlation coefficient: temperature, $r > -0.573$, $P < 0.001$; humidity, $r > 0.593$, $P < 0.001$).

During the cold months (December to February), the foraging activity was mainly reduced to daytime hours and correlated highly with the environmental temperature (Pearson's correlation coefficient: $r > 0.623$, $P < 0.001$). The foraging activity on the tree trunk stopped completely below 5°C (Fig. 1). However, there was no association between environmental humidity and the daily foraging activity during these months (Pearson's correlation coefficient: $r < -0.299$, $P > 0.1$).

Seasonal Foraging Activity on Cork Oaks. The foraging activity of the Argentine ant on cork oaks was continuous throughout the year (Fig. 2). However, in the colder months, it was much lower in comparison with the rest of the year. In May, it seemed to increase

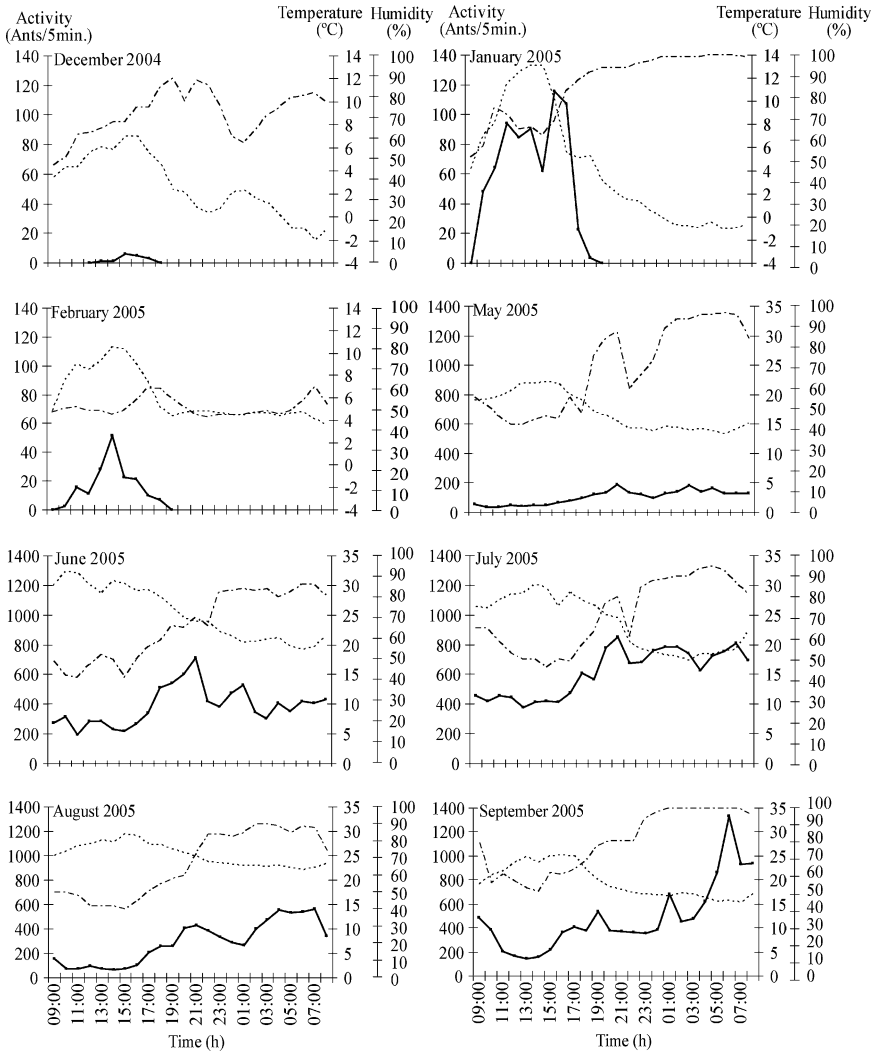

Fig. 1. Average daily foraging activity (number of ants during 5 min) of the Argentine ant on five cork oaks during the warm and cold period. Solid line, average foraging activity of workers; dotted line, air temperature registered each hour during sampling; dashed line, relative humidity recorded each hour during sampling.

until June and July, which are the months with maximum foraging activity, followed by a sudden decrease in August. There was a new rise in September, and after this period, the foraging activity gradually declined with the environmental temperature. We found a positive correlation between the temperature and the seasonal foraging activity on cork oaks (Pearson's correlation coefficient: $r = 0.729$; $P < 0.001$; Fig. 2), whereas there was no association between the seasonal activity and the average humidity registered during the sampling hours (Pearson's correlation coefficient: $r = -0.177$; $P > 0.1$).

In the noninvaded trees, the only species present were the native ants *Crematogaster scutellaris* (Olivier) and *Lasius cinereus* Seifert.

The native ant's seasonal foraging activity on cork oaks was always lower than the seasonal foraging activity of the Argentine ants (Figs. 2 and 3). In addition, the native ants studied had a hibernation period from late November until the beginning of springtime (March), whereas the invaders did not have any hibernation period.

Liquid Food Collection from Cork Oaks. The daily amount of liquid food collected by the Argentine ants during the winter months was quite low in relation to the rest of the year (Fig. 4). After this period, liquid food collection increased until June and July, which were the months of maximum liquid collection. From those months on, the daily amount of liquid food collected decreased gradually until December, with a small peak in October.

Argentine ants collected more liquid food than the native ants during the hibernation period of the latter (November to March), and also during the months previous to this period and the months that followed it. However, the native ants collected more liquid food

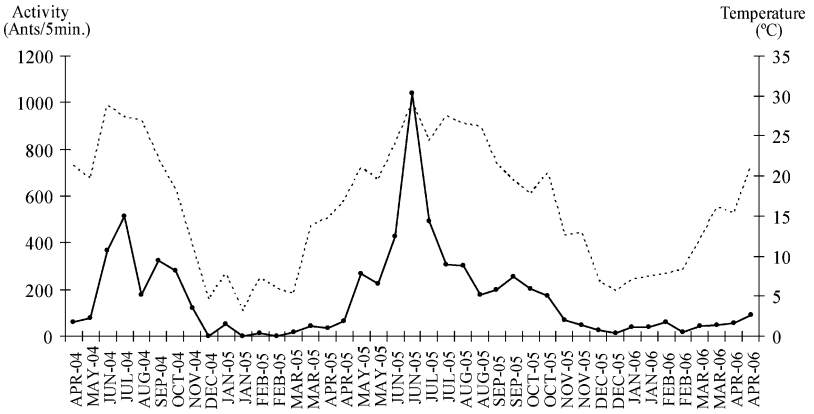

Fig. 2. Seasonal foraging activity on cork oaks by the Argentine ant. Solid line, average foraging activity of workers (number of ants in a 5-min period) during the sampling day on five cork oaks; dashed line, average daily temperature during the sampling day.

than the Argentine ants during their periods of maximum activity (May to August). Nevertheless, these differences were barely noticeable for most of the year (Fig. 4).

The seasonal foraging activity pattern of the Argentine ant was closely related to the seasonal fluctuations of the estimated amount of liquid food collected in 24 h.

Solid Prey Captured by the Argentine Ant on Cork Oaks. The Argentine ants (Fig. 5) foraged for solid prey on cork oaks throughout the year except on the coldest days when foraging was null. Despite this almost continual effort, foraging of solid prey was quite low because, even in the periods of maximum solid prey collection, <6% of workers that returned to the nest carried solid prey between their mandibles.

Spring (March to May) was the season of maximum foraging of solid prey, followed by a gradual downward slope until July, which was the month of minimum solid prey foraging. There was another period of active foraging in autumn (September to December) with a peak in October.

Argentine ant workers collected a diversity of prey from the cork oaks (Table 1). The vast majority of prey was arthropods, both adult and immature forms. Among the immature forms, all the prey was insects, whereas there were some arachnids among the adult forms. There were also a small proportion of vegetal remains (<2% of the total sample). The main order collected was the order Sternorrhyncha. Within this group, almost all the samples were aphids. Some samples showed an advanced dehydration level, and others were still alive when they were collected.

Discussion

The Argentine ant shows seasonal variation in daily foraging activity patterns on cork oaks. During spring and summer the foraging activity is continuous, around the clock. This continual activity by *L. humile* has also been observed in California by Human et al. (1998). The native ant species studied, *C. scutellaris* and *L. cinereus,* also have a continual foraging activity pattern on cork oaks similar to that of other ant species

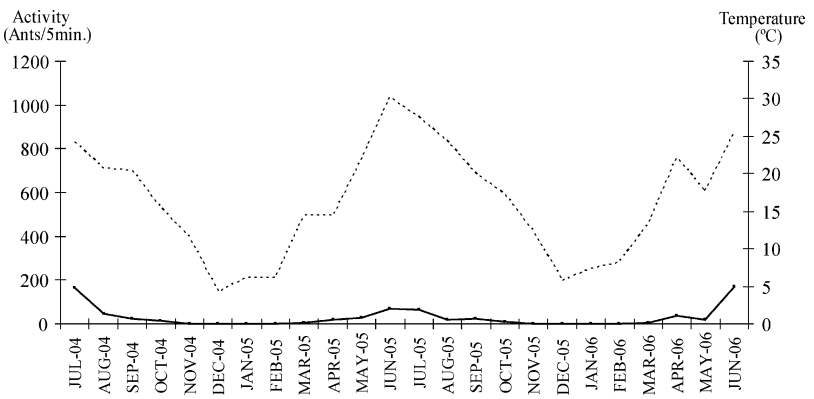

Fig. 3. Seasonal foraging activity on cork oaks by the native ants studied: *C. scutellaris* and *L. cinereus.* Solid line, average foraging activity of workers (number of ants in a 5-min period) during the sampling day on five cork oaks; dashed line, average daily temperature during the sampling day.

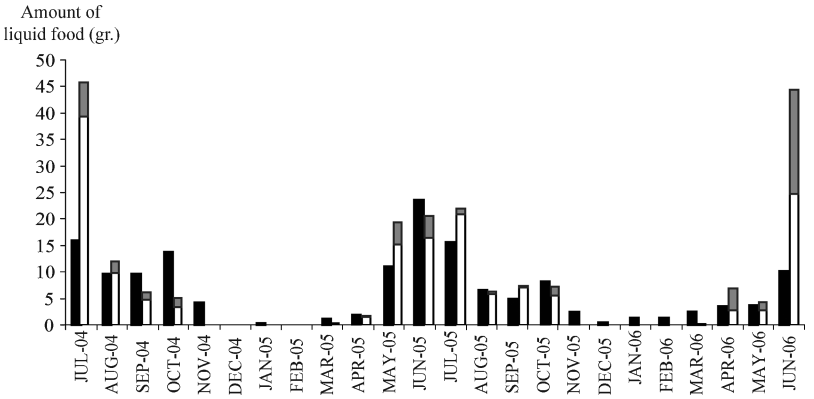

Fig. 4. Estimated amount of liquid food collected in 24 h by the Argentine ant (black bars) and the native ants studied (white and gray bars): *C. scutellaris* (white bars) and *L. cinereus* (gray bars) on five cork oaks.

such as *Camponotus cruentatus* (Alsina et al. 1988), *Iridomyrmex purpureus viridiaeneus* (Greenaway 1981), and *Camponotus detritus* (Curtis 1985). Some authors have attempted to explain this behavior by pointing out that aphids produce honeydew continuously throughout the day and the workers tend to collect it at the same rate.

In the days of continual food gathering, the Argentine ant's foraging activity on cork oaks is greater at night. This behavior is related to the abiotic factors studied (humidity and air temperature). It seems that the daily foraging activity of the Argentine ant on cork oaks during spring and summer days is limited by lower humidity and higher temperatures. Changes in these two factors can lead to changes in the daily activity pattern of this species. For this reason, we believe that the continual foraging activity observed during the spring and summer days can be explained by the abiotic conditions that occur throughout these months, which allow food gathering over a 24-h period.

As in other ant species (Sanders 1972, Bernstein 1974, Alsina 1988), the winter foraging activity on cork oaks became exclusively diurnal and was related to temperature but not to relative humidity.

Below 5°C, the Argentine ant stops its foraging activity on cork oaks completely. Our results are in agreement with the results of Markin (1970a).

Whereas the native ant species studied have a hibernation period from November to March, the Argentine ants do not have any hibernation period and are busy as long as the air temperature allows it. This complete lack of a period of hibernation for *L. humile* was also reported by Benois (1973) in the Antibes region (French Riviera) and Holway (1998b) in northern California.

The seasonal foraging activity pattern of the Argentine ant on cork oaks is closely related to the seasonal fluctuations in the amount of liquid food collected by the workers. This may result from the fact that the main food source collected by this species is liquid food (Markin 1970a).

The Argentine ant gathers liquid the whole year round. This behavior could be related to a lack of stored food caused by the great availability of liquid food throughout the year in the trees, basically honeydew secreted by hemipterans.

Despite this continual liquid extraction, the average amount of liquid food introduced into the nest by the Argentine ants during the winter months was almost

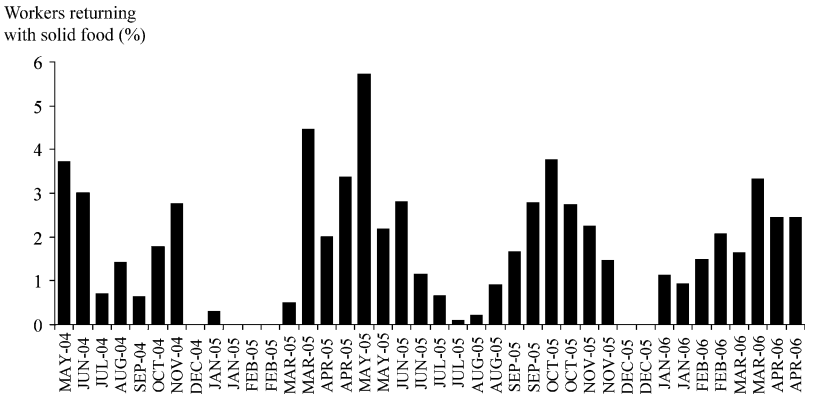

Fig. 5. Proportion of Argentine ant workers returning to the nest with solid food collected from cork oaks.

Table 1. Number and percentage of solid prey taken to the nest by workers of the Argentine ant

Type of prey	*N*	Percentage	Type of prey	*N*	Percentage
Adult stage	439	41.26	Immature stage	552	51.88
Sternorrhyncha	245	23.03	Sternorrhyncha	306	28.76
Thysanoptera	46	4.32	Lepidoptera	114	10.71
Psocoptera	45	4.23	Coleoptera	50	5.43
Hymenoptera	37	3.48	Heteroptera	28	4.70
Diptera	30	2.82	Unidentified nymph	19	1.78
Acarida	13	1.23	Thysanoptera	16	1.50
Coleoptera	10	0.940	Orthoptera	8	0.752
Collembola	8	0.752	Dermaptera	4	0.376
Araneida	4	0.376	Diplura	2	0.188
Orthoptera	1	0.094	Dictyoptera	2	0.188
Unidentified	63	5.92	Hymenoptera	2	0.188
Plant remains	10	0.940	Heteroptera nymph	1	0.094

insignificant. This may result from the low foraging activity on the trees observed during this period, which is most probably caused by the low temperatures. In spring, the daily amount of liquid collected appeared to increase. It seems that this increase is not only related to the rise in the air temperature, but may also be related to the beginning of the reproductive cycle in which the workers increase their own activity to carry out several tasks, such as taking care of the brood or feeding the queens. Moreover, egg laying is strongly influenced not only by abiotic conditions, like temperature or humidity, but also by the amount of food ingested (Benois 1973). The liquid food collected from cork oaks, most likely honeydew, may provide the workers with the necessary energy to carry out their work (Carrol and Janzen 1973). Therefore, it is during these strong work periods when the foraging activity on cork oaks, and consequently the collection of liquid food sources, seems to increase. In June and July, the collection of liquid food is at its maximum. During these months, a large number of males and workers hatch into the nest producing a strong demographic increase (Markin 1970b, Benois 1973). Because the main part of the liquid food carried by the workers is likely to be sugary liquids from hemipteran exudates, and the main consumers of this type of food in Argentine ant nests are males and workers (Markin 1970c), this sharp increase in liquid collection may be related to the workers' need to meet the trophic requirements of these castes.

The second peak of liquid collection in autumn seems to be related to the second reproductive period of this species described by Benois (1973). This new period of intense work would again cause an increment in the amount of liquid food introduced into the nest. After this period, the amount of liquid food collected decreases with the fall in temperature until the following spring, when the cycle begins again. Of course, there could be other possible nonexcluding explanations to the seasonal differences in liquid food collected by the foraging workers of the Argentine ant, such as the seasonal availability of this source on the trees.

Argentine ant workers collect more liquid food from cork oaks than the native ant species during the winter months and during the adjacent months because of the hibernation period of the latter. However, the native ants collect much more liquid food than the invaders during their months of maximum activity from May to July, even though their foraging activity on the trees is lower. These differences are caused by the larger body size of the native species, which allows them to gather larger quantities of liquid than the tiny Argentine ants. We observe that, in general, the Argentine ant workers collect a similar amount of liquid food from cork oaks throughout the year in relation to the native ants studied. Therefore, if we take into account that the direct physicochemical damage produced by the hemipterans can have significant negative consequences for the host plant (Buckley 1987), the possible damage caused by the ant-hemipteran mutualism to the host plant would get neither better nor worse after the invasion. Nevertheless, further research is necessary to assess if the annual or monthly liquid collection by Argentine ants and native ants has a significant negative effect on the growth and reproduction of the host plant and also if there are differences in the amount of plants affected.

We observed two peaks of solid prey foraging during the year on cork oaks. The first occurred from March to June, with a peak in May and the second from September to November with a peak in October. We must consider insects as an important source of proteins. The main consumers of proteins in the nest are larvae and queens because this nutrient is essential for the optimal growth and development of larvae and for the production of eggs by queens (Markin 1970c, Rust et al. 2000). Therefore, the high prey capture values found in spring with the peak in May correspond to the period of maximum oviposition rate of the queens and to the maximum larvae densities in the nest (Benois 1973). The other period of intense foraging effort is in autumn, from September to November, coinciding with a second but weaker oviposition period of the year and with a second maximum amount of larvae in the nest in October (Benois 1973). Thus, one possible explanation for the seasonal variation of solid prey foraging by the Argentine ant workers is that it varies seasonally depending on the colony's demand for protein in relation to its growth phase.

These results are in agreement with the results obtained by Rust et al. (2000) in a California citrus grove.

Edwards (1951) also came to the same conclusion observing the foraging ecology of the ant species *Lasius niger.* The workers of this species focus their attention on protein foods during their period of colony growth when there is a high density of developing larvae in the nest, but during the pupation period of the larvae they prefer to search for carbohydrate food to feed the adults.

The proportion of workers entering the nest with solid prey in their mandibles is quite low (<6%). This value is similar to the values obtained for other ant species (Gotwald 1968, Sanders 1972, Lévieux 1975, Curtis 1985, Alsina et al. 1988); all had a low proportion of workers introducing solid prey into the nest, with values between 3 and 5.9%. Because most workers that enter the nest from cork oaks are carrying liquid food, the explanation for these low values could be that the main food source of Argentine ants is liquid food. Similarly, Markin (1970a) found that ≈99% of the material carried into the nest by the Argentine ant workers in a Californian citrus grove is liquid food.

Small insects, both adults and immature forms, are the main group of prey collected by the Argentine ant workers. The captured prey is mainly dehydrated, although we also observed a small percentage of living prey being transported to the nest. This fact suggests that, in reference to the solid diet, *L. humile* is basically a scavenger ant, but can also occasionally play the role of hunter of small specific insects or tiny apterous forms such as small larvae or aphids. Small insects are also the main source of solid prey of other ant species (Lévieux 1975, Retana et al. 1986). Markin (1970a) also found that a large amount of the solid prey captured by the Argentine ants on citrus trees were hemipterans. He supposed that they were dead when the ants collected them, whereas in this study we found some living aphids being transported to the nest by the *L. humile* workers.

Because >50% of the prey collected from cork oaks by the Argentine ant workers are aphids, it is probable that these are not only protected by the workers for their honeydew source, but are also used as a source of protein. It seems that this behavior is not unique to the Argentine ant: there are other ant species that also collect hemipterans as a protein source and, at the same time, establish mutualistic interactions with them to obtain carbohydrates from their honeydew. This is the case of *Oecophylla longinoda* (Way 1954), *Lasius flavus* (Edwards 1951), *Lasius niger* (Pontin 1958), and *Formica rufa* (Skinner and Whittaker 1981). It has been reported that *F. rufa* preys only on the nonmyrmecophilous species of hemipterans *Drepanosiphum platanoides* (Pontin 1958) and establishes a mutualism with the myrmecophilous species *Periphyllus testudinaceus* (Skinner and Whittaker 1981). By doing so, they ensure a protein intake without harming their sugary sources. This may be a good explanation for the case of the Argentine ant in our study area, although further research on this point is necessary.

The Argentine ant's daily and seasonal foraging activity in a Mediterranean open cork oak secondary forest is strongly related to abiotic conditions, especially to air temperature. Thus, during the coldest months, the foraging activity of this species is limited to the warmest periods of the day, and during the spring and the summer months, their foraging activity occurs mainly at night. Moreover, the Argentine ant workers change their food preferences depending on the phase of the reproductive cycle, collecting more protein food in spring (March to late May) and autumn (September to November) to feed the queens and the developing larvae, and more carbohydrate food during the rest of the year, especially during June and July, to feed the newborn males and workers of the colony. These results are essential for improving current knowledge of the Argentine ant's foraging behavior in invaded natural areas to initiate control methods based on using baits.

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