

More and bigger queens: a clue to the invasive success of the Argentine ant (Hymenoptera: Formicidae) in natural habitats

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Abstract

Understanding the invasion process of an exotic species could be useful to manage its dispersion in natural habitats. To that effect, we provide new data on the queens' biological and physiological characteristics in *Linepithema humile* (MAYR, 1868) colonies from both the invasion front (contact area) and the totally invaded area (invaded area) in order to examine the differences between them. We analyze: 1) queen densities per liter of nest soil, 2) fat content (%), 3) oviposition rates, and 4) the queen / worker thorax volume ratios of individuals from nests situated in the contact and invaded zones. All these parameters are good estimators of the invasive capabilities of colonies, as they are related to dispersion speed and successful colony foundation. Although we did not detect physiological differences in the fat content and oviposition rates of queens from the two zones, we found evidence of differences in the social structure of nests (queen densities) and in the morphology of queens (queen / worker thorax volume ratios) between nests from the invasion's contact and invaded zones. In the former there were bigger queens and higher queen densities than in the latter. Those differences are probably a response to the different ecological contexts of the two zones and would provide the colonies in the contact zone of the invasion with a higher invasiveness potential for competing with the native ant community for empty niches and resources.

Key words: Queen colony investment, fat content, oviposition rate, queen size, queen densities.

Myrmecol. News 18: 19-24 (online 4 December 2012)

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 19 December 2011; revision received 22 June 2012; accepted 3 July 2012

Subject Editor: Philip J. Lester

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Introduction

The Argentine ant, *Linepithema humile* (MAYR, 1868), is a well-known invasive species (LOWE & al. 2000). Native to South America, it has spread worldwide through commercial activities (SUAREZ & al. 2001) to areas with Mediterranean type climates usually associated with human-altered habitats (SUAREZ & al. 1998). However, its ability to invade natural areas with low levels of anthropogenic disturbance is also widely recognized (HOLWAY 1998a, GÓMEZ & al. 2003). In these areas, its effects on the ecosystem are extremely harmful since it negatively impacts native ant faunas (HUMAN & GORDON 1996, 1997, HOLWAY 1998b, SUAREZ & al. 2001) and causes changes to important ecological processes such as seed dispersal (BOND & SLINGSBY 1984, GÓMEZ & OLIVERAS 2003) and pollination (VISSER & al. 1996, BLANCAFORT & GÓMEZ 2005), which in turn produce significant disruptions in ecosystem assemblages.

Attempts to eradicate the invasion from affected natural areas without eliminating the queens, which constitute the reproductive power of the colony, have met with little success (KRUSHELNYCKY & REIMER 1998a, b). Moreover, these methods have employed chemical procedures that are banned in some protected natural areas, making the invasion still more difficult to deal with.

As the probability of success in eradicating an invasive species decreases with an increase in its distribution range

(MYERS & al. 2000), the eradication of the Argentine ant in natural habitats over hundreds of hectare is practically impossible. In such places, slowing its rate of spread by making the elimination of queens the main objective of any control method applied may be the best way to manage the invasion. This is no easy matter due to the species' highly polygynous nature (the presence of more than one queen in each nest) (KELLER 1995) and its unicoloniality (PASSERA 1994), where a lack of territorial boundaries allows it to create a large network of interconnected nests. Successfully eliminating Argentine ant queens in natural invaded environments in a more efficient way requires detailed information about their invasive process related to its physiological and ecological traits. In that sense, we wonder if colonies in the contact zone of the invasion may use more efficient colonizing strategies to increase their invasive potential than those in the invaded zone. If that is the case, the application of control methods to eliminate queens in the contact zone may be more effective than their application in the invaded zone.

Until now there have been few studies of the dynamics of Argentine ant queens in natural environments that could help us answer these questions. INGRAM (2002) observed that nests in the invaded zone of an invasion contained more queens than those in the contact zones. KELLER & al. (1989a) detected an annual execution of queens carried out by their

own workers in May. Additionally, ABRIL & al. (2008a) observed that both this annual execution and the cyclical fission-fusion pattern of nests (HELLER & GORDON 2006) generate a seasonal variation in the Argentine ant queen densities. Whereas in winter queen densities reach their maximum of the year after the establishment of the so called "winter colonies", in summer they reach their minimum, following the creation of the "summer colonies", which are characterized by their small size and lower density of individuals (NEWELL & BARBER 1913, MARKIN 1970, BENOIS 1973, HELLER & GORDON 2006, ABRIL & al. 2008a).

Unfortunately, there is still a lack of information regarding Argentine ant invasion strategies in relation to the queens. This study is an attempt to compare different traits of the biology and physiology of the queens in nests situated at the forefront of expansion (in contact with the native ant population), and nests situated in the totally invaded zone (where the Argentine ant is the only ant present), in order to understand the invasion process in natural environments. Specifically, we want to 1) examine for differences in Argentine ant queen densities in nests from these two areas; 2) examine for differences in the fat content of queens; 3) examine for differences in the queen / worker thorax volume ratio; and 4) compare queen oviposition rates between invasion sites. All these parameters are good estimators of the invasive capabilities of the colonies, as they are directly related to dispersion speed and successfully colony foundation (HÖLDOBLER & WILSON 1977, KELLER & PASSERA 1989, STILLE 1996, BRUNA & al. 2011). Our main hypotheses are as follows:

1) It seems that areas situated at the front of invasion differ in their ecological contexts from the areas situated behind (INGRAM 2002). The former may offer more available nest sites and food resources (INGRAM 2002, TILLBERG & al. 2007), but in contrast, there is a greater competition pressure for these available resources as a result of the native ant community resisting to the invasion. In addition, it seems that increasing queen numbers in a nest is a colony's way to fill empty niches quickly when the environment has a strong competitive pressure (HÖLDOBLER & WILSON 1977). In accordance to this, we hypothesized that the number of Argentine ant queens, and in consequence their oviposition rates, should be higher in nests of the front of invasion (contact zones) than in nests situated behind (invaded zones).

2) Both the fat content of queens and the queen / worker thorax volume ratio seem to be related with a successfully colony foundation (KELLER & PASSERA 1989, STILLE 1996). In the case of the fat content of queens, we hypothesized that queens from the front of invasion (contact zones) should have a higher fat content than queens from behind (invaded zones), as a way to increase their survival and, hence, achieve a successful colony foundation in these high competitive areas. Regarding the queen / worker thorax volume ratio, higher indexes seem to indicate queens with bigger thoraxes (STILLE 1996), and thus, higher long-range dispersals (BRUNA & al. 2011). Moreover, there are evidences of shifts in behavior and morphological characteristics among invasive animals as the cane toads between the invaded and non-invaded areas. It seems that individuals near the front of invasion are bigger and faster, than individuals behind the front. Therefore, the former has higher



Fig. 1: Location of the three study areas (SC: Santa Cristina d'Aro front, PB: Punta Brava front, PD: Pedralta front), Catalonia, Spain. Detailed map taken from the Image Service of the Planet Google Earth™.

dispersion abilities and reach long-range dispersals (BROWN & al. 2007, PHILLIPS & al. 2007, LLEWELYN & al. 2010). Under this background, we expected to find higher queen / worker thorax volume indexes in queens from the front of invasion (contact zones) than from behind (invaded zones).

Material and methods

The samples were taken from three different Argentine ant invasion limits (referred to as fronts of invasion) in invaded cork oak secondary forests: two located at the southern edge of the Gavarres massif, in the areas of Santa Cristina d'Aro ($41^{\circ} 48' 51.71''$ N, $3^{\circ} 01' 50.57''$ E), and Pedralta ($41^{\circ} 47' 31.53''$ N, $2^{\circ} 58' 52.79''$ E), and one in the Cadiretes massif, in the area of Punta Brava ($41^{\circ} 46' 13.51''$ N, $3^{\circ} 00' 17.93''$ E) in the NE of the Iberian Peninsula (Fig. 1).

Prior to the design of the study, bait sampling was carried out on each invaded area to identify the fronts of invasion. For this purpose, tuna and marmalade baits were placed every four meters on random transects of 100 m in length, and the invasion limit was identified by the last bait visited by the Argentine ants.

After identifying the front path, in each of the three areas, we defined the contact zones (where both Argentine ants and native ants are in contact), and the invaded zones (where we found a high abundance of Argentine ants and a low presence of native ants).

The contact and the invaded zones of all three study areas were in close proximity (≈ 1.5 km apart) and had similar environmental characteristics, which meant that possible differences in terms of nest density would not be related to abiotic differences between the two zones.

The dynamics in Argentine ant colonies vary seasonal-

ly (NEWELL & BARBER 1913, MARKIN 1970, BENOIS 1973, HELLER & GORDON 2006, ABRIL & al. 2008a). In winter, nests contain a greater density of queens and individuals as a result of a regrouping process, and in spring they split into smaller nests, with a lower density of queens and workers, as a result of a dispersion process. It is those winter nests that contain the clues to the species' dispersion power in spring and the invasion of new habitats. For this reason all the samples obtained in the present study were taken from winter nests.

Queen density: We estimated Argentine ant queen density per liter of nest soil from January to March 2010, taking samples of two liters of soil from 24 nests in each of the invaded forests mentioned above. Twelve of these nests were from the invaded zones of the invasion, and the other 12 were from the contact zones. In these areas Argentine ants mostly nest under stones, so all the nests sampled were from this kind of nest. In total, we sampled 72 liters of soil from 36 different nests in each zone, contact and invaded.

Once in the laboratory, we manually extracted the queens present in each sample.

Daily oviposition rate of queens: In order to assess if there were differences between the oviposition rates of queens in nests in the contact and the invaded zones, we collected in both Castell d'Aro and Pedralta a total of 24 queens from six different nests in each zone. In the laboratory, we created six artificial polygynous nests with four queens for both the contact and invaded zones. Each nest had the same ratio of workers to queens – approximately 200 workers per queen. All the queens / workers in the artificial nests came from the same nest in the field. The artificial nests were made up of a regular plastic box (180 mm × 115 mm and 35 mm high) fitted with a layer of dry plaster of Paris connected laterally to a smaller box (75 mm × 50 mm and 25 mm high) by a cotton-wool wick permanently in contact with a piece of cotton soaked in water. To prevent escape, the inner sides were coated with liquid PTFE (Fluon®). The ants were fed daily with a variant of the artificial diet described by KELLER & al. (1989b), reported in ABRIL & al. (2008b), which allowed a healthy production of workers and sexuals and high fecundity in queens (ABRIL & al. 2008b, 2010). The nests were incubated at 28°C, the optimal temperature for queen oviposition in the Argentine ant (ABRIL & al. 2008b). After one week of incubation in the laboratory, the queens were subjected to an oviposition test that followed the same procedure as in ABRIL & al. (2008b). In brief, this consisted of isolating the queens individually and some of their workers in test-tube nests for 24 hours. After this period we counted the eggs laid by each queen. The test-tube nests were plastic tubes that used the same mechanics as the nests described above to provide humidity to the individuals. They were 70 mm long × 10 mm in diameter, with a plastic top covered on its inner side by a layer of dry plastic of Paris connected by a wick of cotton wool to a small chamber filled with water. In order to be able to identify each queen throughout study, we marked them with Uni Paint marker pens (Mitsubishi Pencil Co., LTD.) on the dorsal surface of their thorax. The oviposition rate of each queen was measured every four days, for a total of six times. The duration of the study was one month, from March to April 2009, comprising the period when the oviposition of the queens was at its maximum (BENOIS 1973).

Queen / worker thorax volume ratio: During winter 2010 (January to March) we collected a total of 300 queens and 300 workers from eight different nests in the contact zones of the invasion, and 290 queens and 290 workers from 28 different nests in the invaded zones. We made a dried collection of these specimens and then we estimated the worker and queen thorax volumes (length × width × height) in order to determine the queen / worker thorax volume ratio, as in STILLE (1996).

Fat content of queens: In winter 2009 we collected queens from nests situated in the contact and invaded zones of the invaded areas, a total of 161 queens from 15 different nests and 131 queens from ten nests, respectively. We killed them with ethyl acetate vapor in the laboratory and then followed the same procedure as KELLER & PASSERA (1989) based on PEAKIN (1972). We first determined the individual fresh weight of queens, and then dried them at 70°C for 24 hours. After that, we determined their dry weight and extracted the fat with petroleum ether (boiling point 40 - 60°C) and a Soxhlet apparatus over 24 hours. The queens were then dried again at 70°C for 24 hours and weighed. All weights were determined to the nearest 10⁻⁵ g. Fat content was expressed as a percentage of dry weight.

Data analysis: We made all the comparisons between queens from the contact and invaded zones using generalized linear mixed models (GLMMs) with a Poisson error distribution and log-link function for count variables (queen densities, oviposition rates, and fat content) and a Gaussian error distribution with identity log for the rest of the variables. In the case of comparisons between queen densities per liter of soil, the area (Santa Cristina d'Aro, Pedralta or Punta Brava) was used as a random factor and the zone (contact or invaded) as a fixed factor. In the case of the oviposition rate and fat content of queens and the queen / worker thorax volume ratio, we used as a random factor the nest and the zone (contact or invaded) as a fixed factor. We used the R 2.5.1 statistical package (copyright 2001, The R Development Core Team) for all analyses.

Results

Queen density: Our results showed a difference in queen densities per liter of nest soil between the contact and the invaded zone of the invasion (GLMM: $t = -3.508$; $P < 0.0001$) (Fig. 2a). Additionally, the number of workers per liter of soil situated in contact zones also seemed considerably higher than the ones situated in the invaded area.

Daily oviposition rate of queens: The daily oviposition rates of queens from both places were not significantly different (GLMM: $t = 0.4171$; $P = 0.680$; Fig. 2b).

We also calculated the individual contribution of each queen to the daily oviposition of the whole artificial nest. We would expect an individual contribution of approximately 25% of the eggs laid in the whole colony by each queen if the daily egg oviposition were equally distributed. However, we observed that in all cases it was always the same queen that contributed most, as almost in all cases this queen was in charge of more than 25% of the colony's egg laying (Fig. 3a, b).

Queen / worker thorax volume ratio: There were significant differences between the queen / worker thorax volume ratios in the two zones (GLMM: $t = -4.620$; $P < 0.001$; Fig. 2c; mean queen / worker thorax volume ratio of nests in the contact zone / invaded zone of the invasion: $30.2 \pm$

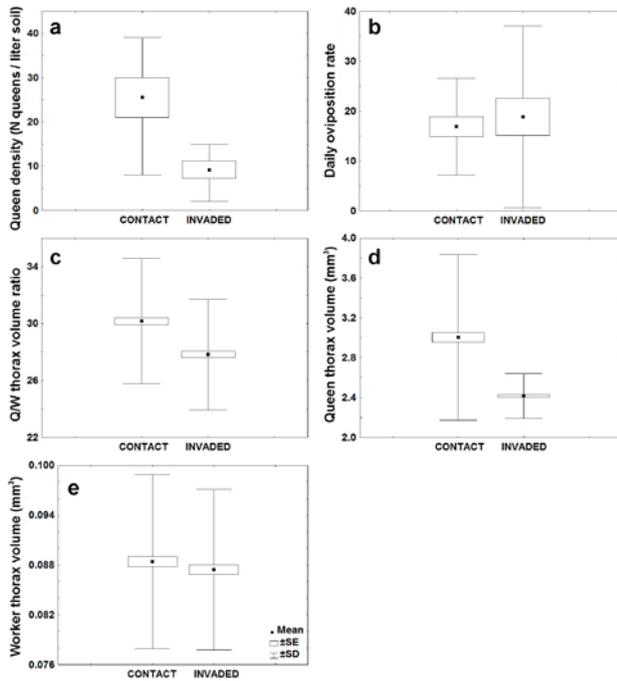


Fig. 2: Queen density of the Argentine ant measured as number of queens per liter of soil (a), Argentine ant daily oviposition rate measured as mean number of eggs / day / queen for six days (b), volume measurements (mm^3) of (c) Argentine ant workers and (d) Argentine ant queens, and (e) queen / worker thorax volume ratio. All comparisons are between nests in the contact and nests in the invaded zones. The error bars are the \pm SD, while the box width corresponds to the \pm SE.

4.25 / 28.0 \pm 3.5; n = 300 / 290). This was due to differences in thorax volumes in queens (mm^3 ; GLMM: $t = -11.25$; $P < 0.001$; Fig. 2d), which were higher in the queens from the contact zones (mean queen thorax volume from nests in the contact zone / invaded zone of the invasion: 2.6 \pm 0.2 / 2.4 \pm 0.2; n = 300 / 290). In contrast, the thorax volumes of workers (mm^3) were the same for the two zones (GLMM: $t = 0.98$; $P = 0.325$; Fig. 2e; mean worker thorax volume from nests in the contact / invaded zone of the invasion: 0.088 \pm 0.01 / 0.087 \pm 0.009; n = 300 / 290).

Fat content of queens: The percentages of fat content in queens between the contact and the invaded zone of the invasion were not significantly different (GLMM: $t = -0.667$; $P = 0.511$). The mean fat content in queens from contact zones was 36% \pm 22 (n = 131), while from invaded zones it was 31.5% \pm 21 (n = 161).

Discussion

According to KELLER & PASSERA (1988), colony investment in gynes can be altered by changing the energy content of each gyne and / or by changing the number of gynes produced. The findings of this study suggest that Argentine ant colonies situated in the contact zone of a natural invaded area make a higher investment of energy in gynes than do colonies situated behind them: These colonies create more and bigger queens. However, the benefits in terms of invasion capabilities of creating more and larger queens remain unclear. It seems that high queen numbers can be considered as a colony's way of adapting to the need to fill

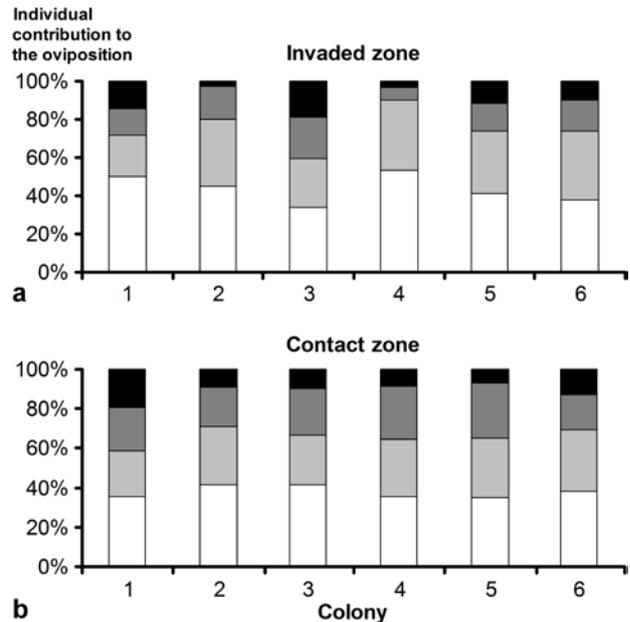


Fig. 3: Individual contribution to the oviposition of the colony (%) from a) nests situated in the invaded zone of the invasion and b) nests situated in the contact zones of the invasion. Each bar section represents the proportion of eggs laid by one of the four queens of the artificial nest (colony) in relation to the total of eggs laid by the four queens in 24 hours.

empty niches quickly (HÖLLDOBLER & WILSON 1977). Thus, these differences in queen densities may be an adaptation to the ecological differences between these two zones. The contact zone of the invasion may offer more available nest sites and food resources than the saturated habitat of the invaded zone (INGRAM 2002). In addition, colonies in the contact zone have to compete with the native ant species resisting the invasion (CASELLAS 2004), consisting of approximately 17 species (M.L. Enriquez, S. Abril, M. Díaz & C. Gómez, unpubl.), some of which highly dominant (CERDÀ & al. 1997). On the contrary, in the invaded zone there is less pressure on colonies to compete for food and nesting sites. This is because the only ant species remaining in the invaded area that is abundant enough to compete with the Argentine ant is *Plagiolepis pygmaea* (OLIVERAS & al. 2005), a subordinate species (CERDÀ & al. 1997) which coexists with the invader in apparent equilibrium (ABRIL & al. 2009). Under these conditions, colonies in the contact zone have to increment their queen densities in order to increase their chances of success in colonizing new areas.

Our results with regard to queen densities do not agree with those obtained by INGRAM (2002) in an invaded natural area of the Haleakala National Park in Hawaii. This may be due to the sampling period. While we took samples in winter to coincide with the period of higher queen densities in the nests (ABRIL & al. 2008a), INGRAM (2002) collected the nests later, likely sampling summer colonies, which are smaller and have a lower density of queens (ABRIL & al. 2008a). This could explain why she found mainly monogynous nests in the contact zone of the invasion, probably because they had recently been founded by queens

who had abandoned their mother nests. Differences between the two studies could also be a consequence of different ecological contexts in the respective contact zones of the invasion. Unicolonial species such as the Argentine ant form colonies of many small nests with few queens in areas where there is little competition or predation, whereas in more competitive environments, larger nests are built because they offer more protection from colony mortality (HEE & al. 2000). The Haleakala National Park is characterized by its relatively few competitive constraints, since the native ant population coexisting with the invader is formed by only two species, and neither is particularly aggressive (INGRAM 2002). This could explain why in this area nests in the contact zone of the invasion had fewer queens and were mainly monogynous.

Our results indicate that queens from the contact zones have bigger thoraxes than queens from the invaded. These results are in agreement with previous studies on the invasive capabilities of cane toads in the front of invasion. They have larger body sizes and relatively longer legs than conspecifics from a long-colonized area, and therefore, greater endurance and longer dispersals (BROWN & al. 2007, PHILLIPS & al. 2007, LLEWELYN & al. 2010). In that sense, in social insects the size of reproductive individuals is associated with dispersal capabilities. Thus, larger-sized queens are associated with long-range dispersal and vice versa (BRUNA & al. 2011). Taking this into account, colonies in the contact zone may invest more energy in creating larger queens so as to ensure new colonies will be established more quickly in these areas following dispersal from the mother nests in spring. However, this is only an assumption, and further research on the relation between bigger queens and longer dispersal on foot among Argentine ant queens is needed to contrast this idea.

Another possible and non-exclusive explanation of these differences in the abundance and size of gynes could be related to the reduction of N-rich protein sources in the areas situated behind the front of invasion, affecting the production of queens through the reduction of their protein intake (TILLBERG & al. 2007).

Data on the fat content of mature Argentine ant gynes reveal that, although values are relatively high for a dependent colony founding queen they fall within the range of data for ants of this kind (KELLER & PASSERA 1989). Additionally, the Argentine ants' thorax volume ratio is quite high, indicating that although they have a dependent mode of colony founding (HEE & al. 2000), their queens' morphology is best fitted to one of independent colony founding (STILLE 1996). This suggests that queens in both the contact and invaded zones of the invasion are morphologically well adapted to carrying out independent colony founding (as their queen / worker thorax volume ratios indicate), but physiologically they are not, indicating there is a halfway point between independent and dependent colony founding.

Curiously, similar results were found for the invasive ant *Lasius neglectus*. This species' colony founding mode is dependent, but it is morphologically qualified to carry out independent colony founding (ESPADALER & REY 2001). As there are no studies reporting the mode of colony founding of native colonies of these two species, could this coincidence be a result of the invading processes of these species in their introduced ranges? To shed light on this question

further research into these species in their natural ranges is needed.

There are no differences between the oviposition rates of queens from nests in the two zones. It seems that an increase in their reproduction capabilities is not a decisive factor in the quicker colonization of new habitats. Moreover, there is always a single queen that contributes most to the oviposition of the colony irrespective of the zone. A previous study on the fecundity of Argentine ant queens proved that in polygynous nests there was always a queen that contributed proportionately more to egg laying than the others (ABRIL & al. 2008b), but the study did not answer the question of whether or not this queen was always the same. We have resolved that question in this study, but further research is necessary to understand the mechanisms that make that particular queen more fertile than the others.

To sum up, the ecological and morphological differences found in the present study regarding the Argentine ant queens seem to respond to the different ecological contexts between the two zones and would provide the colonies in the contact zone of the invasion with a higher invasiveness potential for competing with the native ant community for empty niches and resources.

Acknowledgements

We are grateful to G. Rustullet and G. Vila for their useful advice concerning the Soxhlet apparatus and to Dr. X. Espadaler for his comments on the fat content and queen / worker thorax volume ratio methods. This study was financed by the Spanish Ministry of Education and Science (MEC/FEDER2007-64080-C02-02/BOS and CGL2010-16451). Mireia Díaz acknowledges support from the Spanish Ministry of Science and Innovation for the BES-2008-005102 pre-doctoral grant linked to the CGL2007-64080-C02-02 research project, and Martha Lucía Enríquez from the European Social Fund and the DIUE of the Autonomous Government of Catalonia for her FI pre-doctoral grant.

References

- ABRIL, S., OLIVERAS, J. & GÓMEZ, C. 2008a: Effect of seasonal dynamics on queen densities of the Argentine Ant (*Linepithema humile*) in an invaded natural area of the NE Iberian Peninsula. – *Sociobiology* 51: 1-10.
- ABRIL, S., OLIVERAS, J. & GÓMEZ, C. 2008b: Effect of temperature on the oviposition rate of Argentine ant queens (*Linepithema humile* MAYR) under monogynous and polygynous experimental conditions. – *Journal of Insect Physiology* 54: 265-272.
- ABRIL, S., OLIVERAS, J. & GÓMEZ, C. 2009: Ascertaining key factors behind the coexistence of the native ant species *Plagiolepis pygmaea* with the invasive Argentine ant *Linepithema humile* (Hymenoptera: Formicidae). – *Sociobiology* 53: 559-568.
- ABRIL, S., OLIVERAS, J. & GÓMEZ, C. 2010: Effect of temperature on the Argentine ant's development and survival – an experimental study. – *Journal of Insect Science* 10: 97.
- BENOIS, A. 1973: Incidence des facteurs écologiques sur le cycle annuel et l'activité saisonnière de la fourmi d'Argentine, *Iridomyrmex humilis* MAYR (Hymenoptera, Formicidae), dans la région d'Antibes. – *Insectes Sociaux* 20: 267-295.
- BLANCAFORT, X. & GÓMEZ, C. 2005: Consequences of the Argentine ant, *Linepithema humile* (MAYR), invasion on pollination of *Euphorbia characias* (L.) (Euphorbiaceae). – *Acta Oecologica* 28: 49-55.

- BOND, W. & SLINGSBY, P. 1984: Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. – *Ecology* 65: 1031-1037.
- BROWN, G.P., SHILTON, C., PHILLIPS, B.L. & SHINE, R. 2007: Invasion, stress and spinal arthritis in cane toads. – *Proceedings of the National Academy of Sciences of the United States of America* 104: 17698-17700.
- BRUNA, E.M., IZZO, T.J., INOUE, B.D., URIARTE, M. & VASCONCELOS, H.L. 2011: Asymmetric dispersal and colonization success of Amazonian plant-ant queens. – *Public Library of Science ONE* 6: e22937.
- CASELLAS, D. 2004: Tasa de expansión de la hormiga Argentina, *Linepithema humile* (MAYR 1868), (Hymenoptera, Dolichoderine) en un área mediterránea. – *Boletín de la Asociación Española de Entomología* 28: 207-216.
- CERDÀ, X., RETANA, J. & CROS, S. 1997: Thermal disruption of transitive hierarchies in Mediterranean ant communities. – *Journal of Animal Ecology* 66: 363-374.
- ESPADALER, X. & REY, S. 2001: Biological constraints and colony founding in the polygynous invasive ant *Lasius neglectus* (Hymenoptera, Formicidae). – *Insectes Sociaux* 48: 159-164.
- GÓMEZ, C. & OLIVERAS, J. 2003: Can the Argentine ant (*Linepithema humile* MAYR) replace native ants in myrmecochory? – *Acta Oecologica* 24: 47-53.
- GÓMEZ, C., PONS, P. & BAS, J.M. 2003: Effects of the Argentine ant *Linepithema humile* on seed dispersal and seedling emergence of *Rhamnus alaternus*. – *Ecography* 26: 532-538.
- HEE, J.J., HOLWAY, D.A., SUAREZ, A.V. & CASE, T.J. 2000: Role of propagule size in the success of incipient colonies of the invasive Argentine ant. – *Conservation Biology* 14: 559-563.
- HELLER, N.E. & GORDON, D.M. 2006: Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). – *Ecological Entomology* 31: 499-510.
- HÖLLDOBLER, B. & WILSON, E.O. 1977: The number of queens: an important trait in ant evolution. – *Naturwissenschaften* 64: 8-15.
- HOLWAY, D.A. 1998a: Factors governing rate of invasion. A natural experiment using Argentine ants. – *Oecologia* 115: 206-212.
- HOLWAY, D.A. 1998b: Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. – *Oecologia* 116: 252-258.
- HUMAN, K.G. & GORDON, D.M. 1996: Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. – *Oecologia* 105: 405-412.
- HUMAN, K.G. & GORDON, D.M. 1997: Effects of Argentine ants on invertebrate biodiversity in northern California. – *Conservation Biology* 11: 1242-1248.
- INGRAM, K.K. 2002: Plasticity in queen number and social structure in the invasive Argentine ant (*Linepithema humile*). – *Evolution* 56: 2008-2016.
- KELLER, L. 1995: Social life: the paradox of multiple-queen colonies. – *Trends in Ecology & Evolution* 10: 355-360.
- KELLER, L., CHERIX, D. & ULLOA-CHACÓN, P. 1989b: Description of a new artificial diet for rearing ant colonies as *Iridomyrmex humilis*, *Monomorium pharaonis* and *Wasmannia auropunctata* (Hymenoptera, Formicidae). – *Insectes Sociaux* 36: 348-352.
- KELLER, L. & PASSERA, L. 1988: Energy investment in gynes of the Argentine ant *Iridomyrmex humilis* (MAYR) in relation to the mode of colony founding in ants (Hymenoptera: Formicidae). – *International Journal of Invertebrate Reproduction and Development* 13: 31-38.
- KELLER, L. & PASSERA, L. 1989: Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera: Formicidae). – *Oecologia* 80: 236-240.
- KELLER, L., PASSERA, L. & SUZZONI, J.P. 1989a: Queen execution in the Argentine ant, *Iridomyrmex humilis*. – *Physiological Entomology* 14: 157-163.
- KRUSHELNYCKY, P.D. & REIMER, N.J. 1998a: Bait preference by the Argentine ant (Hymenoptera: Formicidae) in Haleakala National Park, Hawaii. – *Environmental Entomology* 27: 1482-1487.
- KRUSHELNYCKY, P.D. & REIMER, N.J. 1998b: Efficacy of max-force bait for control of the Argentine ant (Hymenoptera: Formicidae) in Haleakala National Park, Maui, Hawaii. – *Environmental Entomology* 27: 1473-1481.
- LLEWELYN, J., PHILLIPS, B.L., ALFORD, R.A., SCHWARZKOPF, L. & SHINE, R. 2010: Locomotor performance in an invasive species: cane toads from the invasion front have greater endurance, but no speed, compared to conspecifics from a long-colonised area. – *Oecologia* 162: 343-348.
- LOWE, S., BROWNE, M., BOUDJELAS, S. & DE POORTER, M. 2000: 100 of the world's worst invasive alien species – a selection from the global invasive species database. – updated and reprinted version of November 2004, Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12 pp.
- MARKIN, G.P. 1970: The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in southern California. – *Annals of the Entomological Society of America* 63: 1238-1242.
- MYERS, J.H., SIMBERLOFF, D., KURIS, A.M. & CAREY, J.R. 2000: Eradication revised: dealing with exotic species. – *Trends in Ecology & Evolution* 15: 316-320.
- NEWELL, W. & BARBER, T.C. 1913: The Argentine ant. – *Bulletin of the USDA Bureau of Entomology* 122: 1-98.
- OLIVERAS, J., BAS, J.M., CASELLAS, D. & GÓMEZ, C. 2005: Numerical dominance of the Argentine ant vs. native ants and consequences on soil resource searching in Mediterranean cork-oak forests (Hymenoptera: Formicidae). – *Sociobiology* 45: 643-658.
- PASSERA, L. 1994: Characteristics of tramp species. In: WILLIAMS, D.F. (Ed.): *Exotic ants: biology, impact and control of introduced species*. – Westview Press, Boulder, CO, pp. 23-43.
- PEAKIN, G.J. 1972: Aspects of productivity in *Tetramorium caespitum* L. – *Ekologia Polska* 20: 55-63.
- PHILLIPS, B.L., BROWN, G.P., GREENLEES, M., WEEB, J.K. & SHINE, R. 2007: Rapid expansion of the cane toad (*Bufo marinus*) invasion front in tropical Australia. – *Austral Ecology* 32: 169-176.
- STILLE, M. 1996: Queen/worker thorax volume ratios and nest-founding strategies in ants. – *Oecologia* 105: 87-93.
- SUAREZ, A.V., BOLGER, D.T. & CASE, T.J. 1998: Effects of fragmentation and invasion on native ant communities in coastal southern California. – *Ecology* 79: 2041-2056.
- SUAREZ, A.V., HOLWAY, D.A. & CASE, T.J. 2001: Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. – *Proceedings of the National Academy of Sciences of the United States of America* 98: 1095-1100.
- TILLBERG, C.V., HOLWAY, D.A., LEBRUN, E.G. & SUAREZ, A.V. 2007: Trophic ecology of invasive Argentine ants in their native and introduced ranges. – *Proceedings of the National Academy of Sciences of the United States of America* 104: 20856-20861.
- VISSER, D., WRIGHT, M.G. & GILLOMEE, J.H. 1996: The effect of the Argentine ant, *Linepithema humile* (MAYR) (Hymenoptera: Formicidae), on flower visiting insects of *Protea nitida* MILL. (Proteaceae). – *African Entomology* 4: 85-287.