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Research article

Queen number in a supercolony of the invasive garden ant, *Lasius neglectus*

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Summary. We have analysed the distribution of queens under stones at the core and at the periphery of a supercolony of *Lasius neglectus* that occupies 14 ha at Seva (NE Spain). Queens were not found alone, but rather within worker groups. Density at the center (mean ± s.d.: 1.38 ± 2.87 queens/stone; n = 100 stones; range 0–14) was not different from density at the periphery (1.18 ± 2.38; range 0–12). The estimate of the number of queens found under stones for the whole colony is about 35500. Egg-laying rates for queens from these two zones were obtained in the laboratory, at three different temperatures, and there were no differences detected. The presence of brood stages, from eggs to cocoons, was also similar in both zones. The homogeneous distribution of colony components may indicate that the area occupied by *L. neglectus* has already reached saturation. With a different technique – soil core extraction – we could estimate the density of workers in the soil: 800 workers per m^2 . Soil cores had 6.28 ± 20.0 workers/core (range: 0–173), giving a rough estimate of 1.12×10^8 workers in the soil, for the entire colony. Though few, some queens were also recovered from soil cores. Queen numbers for the supercolony, based on queens found in the soil, reaches the astounding level of 360000. Numbers are consistent with previous predictions.

Key words: Egg-laying rate, *Lasius neglectus,* polygyny, queen distribution, worker density.

Introduction

The number of queens is a key biological parameter in the sociobiology of ants (Keller, 1993). Unicolonial ants are characterized by high levels of polygyny (Bourke and Franks, 1995) that lead to extremely low within-nest genetic relatedness of workers and queens, posing a challenge for the kinship theory (Bourke and Franks, 1995; Keller, 1995). Unicoloniality – and its origin – has received considerable attention recently, especially in search for an evolutionary explanation of one of the most astonishing facets of this social structure, the absence of aggression between members of the colony, even from widely separated nests. Proximate mechanisms underlying this reduced aggression are still disputed (Giraud et al., 2002; Tsutsui et al., 2003). One system that has potential to help unravel the origin of unicoloniality is a recent invasive pest ant, *Lasius neglectus* (Seifert, 2000; Dekoninck et al., 2002; Espadaler and Bernal, 2003). This unicolonial species has many of the typical tramp ant characteristics (Passera, 1994). It is found in disturbed or highly degraded habitats, has many queens, disperses by budding, and has relatively small workers (Van Loon et al., 1990; Tartally, 2000; Seifert, 2000) in which reproductive egg laying cannot be detected (Espadaler and Rey, 2001). At three known NE Spanish populations ants are invading urban premises, and have attained pest status (locations: Matadepera, Seva, Taradell). According to what is known about several supercolonies of *Lasius neglectus*, a nuptial mating flight is absent and colonies grow by accepting their own young queens after insemination by local males inside the nest (Van Loon et al., 1990; Espadaler and Rey, 2001; Seifert, 2000), although this last author reported that some individuals were found in a spider web. No nuptial flight has ever been recorded in North East Spain. Private property owners do not remember having ever seen drowned sexuals in their swimming pools surrounded by lawns occupied by *L. neglectus*. Thus, the absence of a dispersal flight means that the colony can only develop by a slow expansion of the edges and by budding. A further source of infestation and/or expansion of the supercolony could be by the exchange of infested flower pots between neighbours; thus, a human mediated influence cannot be dismissed.

Boomsma et al. (1990) studied the Budapest colony with an allozyme analysis, and detected very low colony relatedness. From their analysis they deduced: i) there is probably a very huge number of queens in the center of the colony (their Fig. 2) and, due to a differential spatial distribution of allele frequencies, ii) a lesser degree of polygyny towards the edges of the distribution. Here we have tested this in more detail in a Spanish population. A first step was to assess if there were any differences in the presence of queens and the number of queens in the core of the colony and the periphery. This test is relevant because we now know that young queens could, in principle, migrate from their eclosing sites, to carry out short distance nest buds or to independently found new colonies (Espadaler and Rey, 2001), thus providing eggs and new workers for the slowly expanding colony edges. We further explored this possibility by comparing the egg-laying rates of queens from the core and periphery of the colony. Older queens have a higher egg laying rate (Espadaler and Rey, 2001); hence measuring egg laying here is an indirect way of measuring the queen's age in the different zones. As the growth of the colony occurs by expansion and budding (Van Loon et al., 1990; Espadaler and Rey, 2001), additional differences, such as in the presence of cocoons of sexuals, and other brood stages, might be expected between the two zones and were therefore compared in this study.

We used the above mentioned information on queen densities and distributions to infer the colony queen number: it is enormous. We are aware of few earlier attempts to quantitatively assess the number of queens from other supercolonial ants: Newell and Barber (1913) mention 10–20 queens of the Argentine ant under large trees, and Horton (1918), in the same species, detected 13 queens/m^2 in a Californian fruit plantation. Ingram (2002 a, b), by using genetic analyses, detected a variation in queen number per nest – from 0 up to >60 – and this was related to nest densities. Rosengren et al. (1993) counted >500 queens/nest in *Formica aquilonia* or >300 in *F. uralensis* and Higashi and Yamauchi (1979) estimated $>10^6$ to be the number of queens in a supercolony of *Formica yessensis*. The absolute queen number, in itself, may be of limited interest but considered jointly with the egg-laying rate – which varies according to queen age, colony size and temperature (Hölldobler and Wilson, 1990; Williams, 1990) – it can provide an estimate of the potential for colony growth and thus, for the potential future expansion of pest ants.

Material and methods

All counts, measurements and comments refer exclusively to the population from Seva (Barcelona, Spain; 41°48′N, 2°16′E; elevation 650 m; annual rainfall 775 mm). The oldest dates from which inhabitants remember these ants being a problem are from 1985. Such knowledge is lacking from other populations, both in Spain and elsewhere, and these sites may have different properties according to differences in ecological context or climatic conditions. The periphery of the colony was loosely defined as <20 m from the edge; usually the first 10 m allowed for sufficient sampling. The edge was detected through visual inspection of the soil, soil digging with a showel or by looking for cracks in concrete with soil debris, and always checking the identity of the ants.

Density of stones with workers

The number of stones with workers was assessed by counting the number of stones present in 45 randomly chosen squares distributed over the are of the whole population; 14 squares were in the periphery, and 31 in the center. Squares of 5 m × 5 m were delimited and every stone (size >5 cm) was counted and noted if worker ants were present. Squares are assumed to be independent samples.

Queen abundance

We compared the presence and abundance of queens at the center of the supercolony and at the periphery (Fig. 1). In ants, queens have a retinue of attending workers; therefore, before the appearance of sexuals, we did not expect to detect isolated queens without workers. We turned over stones no smaller than 5 cm in diameter (= length + width/2) and noted the presence or absence of queens, workers, eggs, larvae, and cocoons. When queens were present it was also noted how many there were. We continued until 100 stones with workers had been censused in each zone. Each stone was measured at its longest width, length and height, to control for a possible relationship between stone size and the presence of any of the stages noted above. Censuses were done in late April and early May 2002, before the appearance of the new generation of sexuals in June. In addition to the number of queens under stones, the density of queens elsewhere was assessed by soil sampling with a manually operated soil auger that extracted a volume of approx. 300 cm^3 (10 cm diameter, 15 cm deep). This procedure has already been used by Boomsma and Van Loon (1982) to estimate worker populations of underground ants. At 50 random points, distributed over the area of the whole population, we extracted four soil cores at the corners of a 1 m square. Soil was crumbled over a white plastic box (25 × 40 cm), and ants (queens, workers) were counted. This also allowed a gross estimation of the total number of workers in soil for the whole colony.

Egg-laying rates

Laying rates were obtained in the laboratory. In late May, and before the appearance of the sexuals, we collected queens from the central zone and from the periphery. Thus, queens were at least one year of age. Each queen was isolated with 5 workers in tube nests, fed an artificial diet and the eggs were counted one and three days later. Nests were maintained at three different temperatures (25 °C, 28 °C and 31 °C). Ten replicates were established per temperature and for each colony zone. Eggs were counted under a dissecting microscope. After the egg-laying test, live queens were individually weighted.

Statistics

The number of queens under stones and egg laying rates

The number of queens under stones in the two zones was strongly skewed and no transformation achieved or approximated normality. Thus, we used two non-parametric approaches: First, a simple Mann-Whitney test and second, a bootstrapping procedure (1000 random replicates) to estimate the mean number of queens. By doing this we got a distribution that gives a reasonable approximation of the limits of variation for the mean (Efron and Tibishirani, 1993). For both analyses, we used 'zone' as the independent variable and the raw number of queens as the dependent variable. An attempt to estimate the total number of queens in squares of 5 m × 5 m and confidence limits was also done with bootstrapping: a random sample with replacement and with the same sample size for each distribution (sample size = 200 for the number of stones with workers and with/out queens and sample size = 45 for the number of occupied stones in 25 m^2)

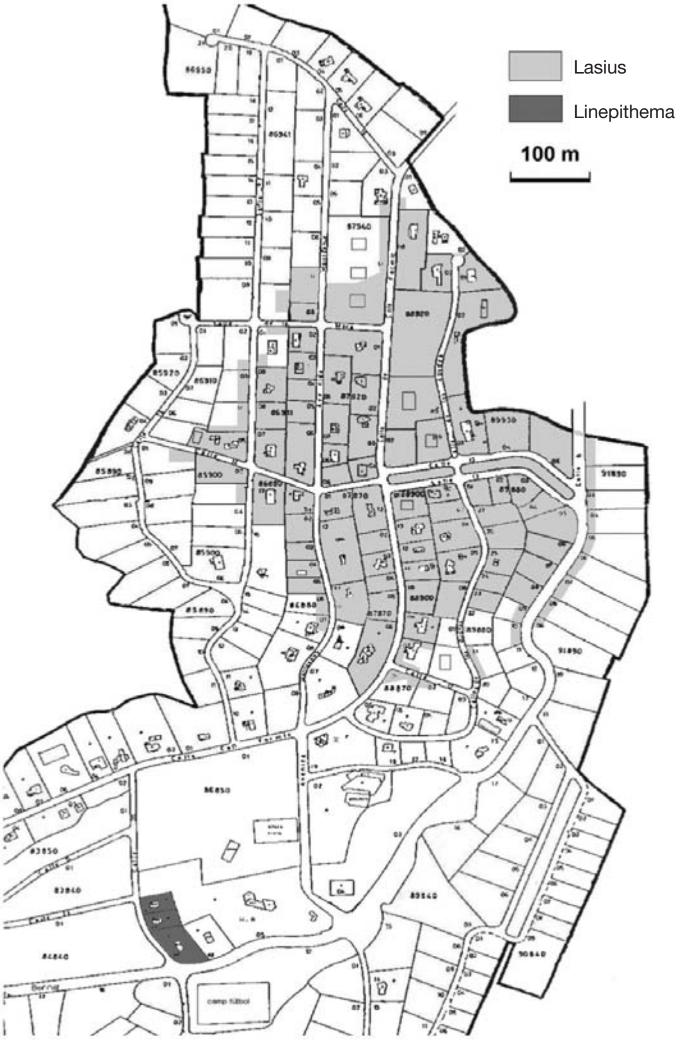

Figure 1. Extension of the *Lasius neglectus* colony in the population of Seva (NE Spain). Data up to May 2003. A more recent, very small population of the argentine ant (*Linepithema humile*) occurs just south of the colony

was done and the means for each sample multiplied so as to get a measurement of the number of queens in 25 m^2. This was repeated 1000 times. Egg laying rates of queens from different colony zones were compared with a repeated measures ANCOVA, with zone (center, periphery) and temperature (25 °C, 28 °C, 31 °C) as fixed factors, and queen fresh weight as a covariate.

Brood stages

To test if workers relocate the brood stages towards the periphery through local migrations, to provide a task force for the colony expansion, eventual differences in the presence of the different stages (eggs to pupae) in the two zones (center vs. periphery) were analysed using a Generalized Linear Model (GLM), with presence-absence as the response variable (binomial variate). Colony zone was used as a categorical factor in the model and stone volume as a continuous predictor. The model included a binomial error structure and a logit link function.

Binomial confidence intervals for the proportion of stones with the various developmental stages were calculated according to Rohlf and Sokal (1995; Table P). The five tests are clearly a family of related tests, addressing the common null hypothesis of there being no difference between the center and the periphery. This situation requires adjustment for multiple tests (Chandler, 1995; Rice, 1989). Routines for the bootstrapping were done using Simstat and Matlab; other statistical analyses were run with Statistica 5.5.

Results

Queen density

Roughly one third of the stones had workers under them (Table 1). When queens were found under stones, they were always attended by workers: no isolated queens were detected. Stone size, as expected, was correlated with queen number although volume explained only 6.25 % of the variance. The number of queens per stone at the periphery (mean ± s.d.: 1.18 ± 2.38; n = 100) was not different (Mann-Whitney U test, two tailed; U = 4982; Z = 0.05; p = 0.95) from that in the central zone (1.38 ± 2.87; n = 100) (Fig. 2); comparisons using bootstrapping did not show any difference between queen number either: the probability of obtaining the observed difference of 0.2 queens, or bigger, is > 0.59. Therefore, for the estimation of the total number of queens in squares of 5 m × 5 m and its variation, we used the global mean of 1.28 ± 2.63 queens per stone; ranging from 0 to 14 queens (n = 200 stones with workers). Queens in the soil were collected only in three of the 200 soil cores. Two cores had a single queen and in a third, we recovered two queens (one alive, and one dead which had been cut in half).

Estimation of queen and worker number

We obtained a cumulative estimate of the queen number by summing estimates from densities under stones and of queens in the soil. Both estimates are very different and are treated separately. By using data of queens under stones, the bootstrapping procedure produced a mean ± s.d. of 6.34 ± 1.79 queens under stones per area of 25 m^2. Confidence limits (± 95 %) of this mean value are 3.34 and 10.17 (Fig. 3). In the Argentine ant in urban settings nests are more abundant *under* pavements (Passera, pers. comm.) and we have often seen workers of *L. neglectus* coming out from cracks with soil debris in roads. So, we have not discounted the surface occupied by pavements and roads (4 ha) from our calculations. As the supercolony occupies at present an area of 14 ha, this number would lead to an estimate of 35504 ± 10024 queens for the total number of queens under stones. From the 200 soil cores extracted only three – from three dis-

Table 1. Stone density and occupancy by ants *Lasius neglectus* at Seva (NE Spain). (n = 45 randomly chosen squares distributed over the whole population; 14 squares were in the periphery and 31 in the center)

	Total stones	+ workers	– workers
Mean	16.64	4.97	11.66
s.d.	24.24	8.11	17.40
Median	7	2	7
Range	0–127	0–42	0–85
Total	749	224	525

Neither the number of stones found at the center and at the periphery (ANOVA: $F_{1,43} = 0.008$; $P = 0.92$) nor the number of stones with workers (ANOVA: $F_{1,43} = 1.3$; $P = 0.25$) were different.

tinct plots – showed positive for queens: two had a single queen and the third had two queens. We accept that 200 cores is probably too small a sample for an accurate estimate; the interesting point, however, is that these samples show that queens do not need the protection of a stone and may be found in the soil throughout the habitat, without any visible marker of their presence at the surface. Given the area of the extracting device (78.5 cm^2), extrapolation of the entire 14 ha of infested area, gives an astounding number of 356580 queens in the soil.

Workers were found in 35 of the 50 random points and in 84 of the 200 cores (four per point), indicating a rather uniform presence over the whole occupied area. This last sample unit had a mean ± s.d of 6.28 ± 20.0 workers/core (range: 0–173), giving a rough estimate of 1.12 ± 10^8 workers in the soil, for the entire colony (workers foraging in trees are not included).

Brood distribution

Stones with eggs, small (= worker + male) cocoons, big (= queen) cocoons and queens were not more frequent in either zone (Table 2). Across the colony, 78.5% of all sampled stones had some brood stages present and 44% had brood stages but no queen was detected. Larvae were found to be statistically more abundant at the center of the colony (P = 0.04). A Bonferroni correction made all differences non-significant.

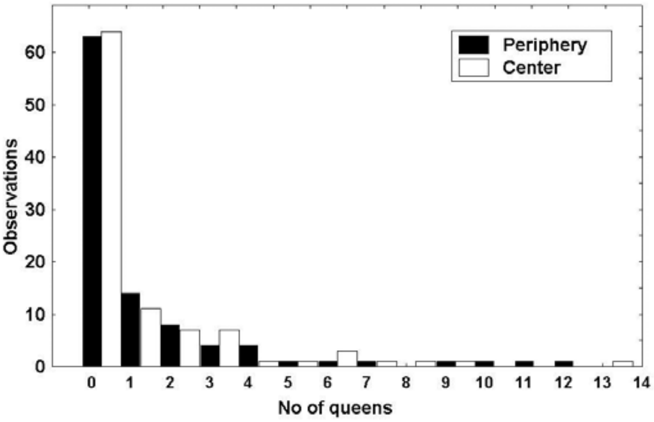

Figure 2. Frequency distribution of the number of queens of *Lasius neglectus* under stones with workers, at the central zone and the periphery of the colony. (n = 100 stones with workers per zone). Population of Seva (province of Barcelona, Spain). Mean ± s.d: 1.38 ± 2.87; n = 100; center. Mean ± s.d.: 1.18 ± 2.38; n = 100; periphery

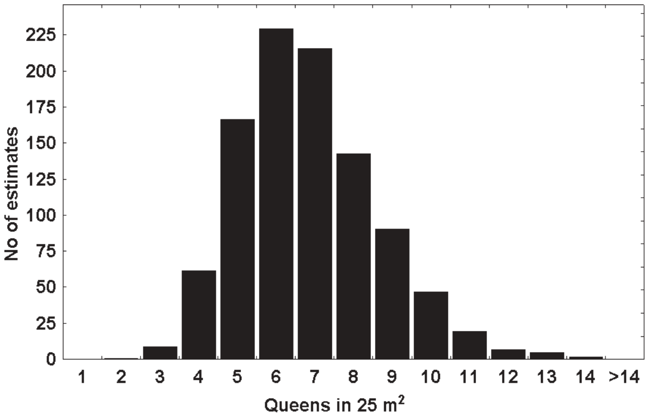

Figure 3. Distribution of bootstrappings (n = 1000) estimating the total number of queens in 25 m^2. Each entry is a replicate of a bootstrap of the mean number of queens per stone (based on 200 stones with workers) × the mean number of stones with workers (based on 45 squares of 25 m^2). Numbers along the X-axis indicate the upper class limits. Mean ± s.d.: 6.34 ± 1.79

Table 2. Distribution of the brood stages and queens. Figures indicate the number of stones at two colony zones (central part vs. periphery) (n = 100 stones/zone) with a given brood stage or queens (presence/absence). Binomial confidence limits calculated according to Rohlf and Sokal (1995; Table P). P indicates before Bonferroni corrections differences in a generalized linear model that included stone volume as continuous predictor (see text)

	Eggs	Larvae	Small pupae	Big pupae	Queens
Center	23	81	14	18	36
95% confidence limits	15–32	72–88	8–22	11–27	27–46
Periphery	23	64	10	21	37
95% confidence limits	15–32	54–73	5–17	14–30	28–47
P	0.81	0.04	0.22	0.60	0.36

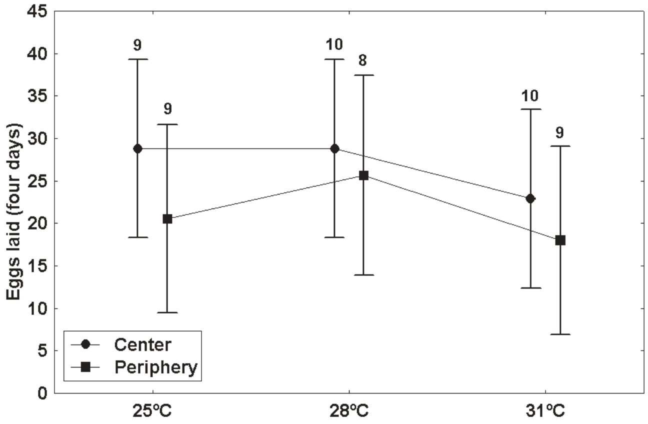

Figure 4. Egg laying rates of queens of *Lasius neglectus* from the center and the periphery of the colony set at three temperatures. Mean ± s.e. Figures on top indicate the number of replicates

Egg-laying rates and weight of queens

Four queens died during the observations and four did not lay any egg. For the remaining 52 queens neither zone ($F_{1,44}$ = 2.5; P = 0.11) nor temperature ($F_{2,44}$ = 0.10; P = 0.90) had any effect on the egg-laying rate during four days (Fig. 4). Queens laid a mean ± s.d. of 24.2 ± 16.3 eggs in four days. The fresh weight of queens from the center (mean ± s.d.; 8.21 ± 1.34 mg; n = 28) was not different (t-test; t = 0.15; P = 0.87) from the weight of peripheral queens (8.27 ± 1.41 mg; n = 24).

Discussion

The spatial pattern of the colony components (queens, workers, brood stages) has been rarely addressed in unicolonial ants. Recently, Ingram (2002a, b) showed spatial flexibility in the social structure of the Argentine ant in several populations in Hawaii: queen number, nestmate relatedness and nest size change along a gradient of time and distance from the edge of the invasion. The ecological context, ephemeral nest sites, nest densities, competitive interactions or frequently disturbed habitats, could be responsible for that variation. That population, though, occupies a very large area (~330 ha) and was detected >30 years ago. In the colony of *Lasius neglectus* studied – occupying a much smaller area and detected >15 years ago – we did not find any asymmetry in queen distribution at the center or the periphery. The degree of polygyny, egg laying rates of queens from distinct zones and the presence/absence of brood stages (eggs to pupae) were also not detected to be different. Boomsma et al. (1990) detected some viscosity in the Budapest population of *L. neglectus*, corresponding to a significant worker relatedness of 0.14, although its significance depended on the scale of observation and density of sampling. Here we do not expect differences in brood density at the center or at the periphery unless some kind of differential transport of brood elements operates. Although it is possible that mated queens, old and young, undertake some limited horizontal displacements, the large colony size, over a big surface, allows for possible genetic structuring within the colony. One consequence of that eventual brood transfer would be to homogenize genetic relatedness. A genetic study at a microgeographical range of the Seva population is needed to address this question. The discrepancy with Ingram's studies could be explained by assuming that the whole area occupied by *L. neglectus* is already saturated immediately after expansion, that all nesting opportunities are now filled, and that only the opening of new habitats, following complete urbanization, allows colony expansion. Studies of other populations are needed to address plasticity in the social structure of *L. neglectus.*

The density of workers is not much different from what is known about other *Lasius* species (Table 3). Notwithstanding, since regions, biotopes and methods to estimate density are multifarious, direct comparisons are suspect. In particular, it has been shown that ant abundance increases with net primary productivity (Kaspari et al., 2000) and specific identity is also of major concern (Kaspari, 2001). This renders a useful comparison of these numbers problematic. It is worth noting that we found workers in 84 of the 200 soil cores, indicating a rather regular presence of workers over the whole surface occupied by the colony. Estimates of worker density in soil for other NE Spanish populations of *L. neglectus*, from different ecological conditions, are currently planned.

Based on relatedness deduced from allozyme variation, Boomsma et al. (1990; their Fig. 2) developed a model relating queen number and frequency of intranidal mating. They showed that 'nearly exclusive intranidal mating would require hundreds of coexisting nest queens'. Their figures

Table 3. Density of workers of several *Lasius* species (workers per m^2)

Ant species	Region	Density	Author
L. niger	Denmark	1590	Nielsen, 1974
L. niger	Schiermonikoog island	15–1339	Boomsma and Van Loon, 1982
L. psammophilus (as *L. alienus*)	Denmark	2100–5068	Nielsen and Jensen, 1975
L. alienus	Berkshire	1167–6398	Waloff and Blackith, 1962
L. flavus	England	420–1130	Odum and Pontin, 1961
L. flavus	Schiermonikoog island	3573–7448	Boomsma and Van Loon, 1982
L. flavus	Yorkshire	13	Pickles, 1940
L. neglectus	NE Spain	800	this work

even show a queen number of thousands when intranidal mating is absolute. Our data on queen numbers fit their prediction exactly. The colony studied is one large, single colony that occupies a sharply limited area (Fig. 1) and, within its limits it is difficult to determine individual nests. It is highly likely that the colony has grown during >15 years – inhabitants remember the ants from approximately the year 1985 on – without input gene flow. The closest other colony of this species (Taradell) is 9 km away as the crow flies and both are likely reproductively isolated, unless humans transport the ants, given the absence of nuptial flights in this species. Thus, we assume the growth of both supercolonies has been largely independent, although the possibility remains that both initiated from the same source. Molecular analyses should provide information on the actual relationships between these colonies. Gene flow remains an affair within the colony. Mapping of colony limits from 1999 to 2003 shows that expansion is an ongoing process and that it is strictly limited to the periphery. No buds have been detected further away in four years, except for an isolated transport of soil from within the colony that was immediately chemically treated and eliminated.

The invasion of new habitats is a complex process, with many factors involved (Walters and MacKay, 2003). In the population of *Lasius neglectus* studied it is highly likely that expansion is enhanced by the construction of premises in the urbanized lots. The process involves the following steps: i) clearing and elimination, usually by in situ burning of cut vegetation; a majority of trees are left untouched; ii) construction of buildings; iii) gardening introducing soil, planting of green and ornamental plants and bushes. Inhabitants provide sufficient summer irrigation to maintain vegetation – and the ants – in good health. If we consider that at the periphery, in the area that has not been invaded, 27 ant species have been detected (unpub. obs.), we hypothesize that these species have been displaced by urban development, leaving an enemy free space (Sax and Brown, 2000) for *L. neglectus*, which may then expand and colonize these new habitats. There, with little or no competition, ants can exploit local trees and their whole complement of aphids, as the studied population they do, from late April to late September, on a 24/7 schedule (unpub. obs.). An alternative hypothesis for the absence of differences between the center and the periphery in all measured variables could be that the resolution of the study is not small enough to detect any potential change in density at the edge, or that the edge, as defined here, was too large to detect any difference. A more detailed study of the edge might give important additional data. Also, the measuring of foraging distances from the edge might shed light on the mechanisms – if any – of competition between *L. neglectus* and native ants. If native ants suffer a lot from the interaction with *L. neglectus*, the ring created around the colony could be quickly inhabited by new bud nests.

The small number of soil cores that contained queens offers limited information and the estimate of the total queen number for the colony through soil cores is to be treated with caution. Notwithstanding, the order of magnitude for the total number of queens, is between 10^4 (estimates using sampling under stones) and 10^5 (estimates by soil cores), and this is consistent with the model derived from genetic studies on the Budapest colony (Boomsma et al., 1990; their Fig. 2) describing the relationship between the frequency of intranidal mating and the number of queens.

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