

Honeydew collection by the invasive garden ant *Lasius neglectus* versus the native ant *L. grandis*

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Abstract Honeydew collection performed by the invasive ant *Lasius neglectus* and by the native ant *L. grandis* was compared. The invasive ant collected 2.09 kg of honeydew per tree while the native ant collected 0.82 kg. The aphid *Lachnus roboris* was visited by both ant species. In holm oaks colonized by *L. neglectus*, aphid abundance tended to increase and its honeydew production increased twofold. The percentage of untended aphids was lower in holm trees occupied by *L. neglectus*. As tending ants also prey on insects, we estimated the percentage of carried insects. The native ant workers carried more insects than the invasive ant. Both ant species preyed mainly on Psocoptera and the rarely tended aphid, *Hoplocallis picta*. We conclude that the higher honeydew collection achieved by *L. neglectus* was the consequence of (1) its greater abundance, which enabled this ant to tend more *Lachnus roboris* and (2) its greater level of attention towards promoting an increase of honeydew production.

Keywords Aphid–ant mutualism · Invasive ants · *Lachnus roboris* · *Quercus ilex*

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Introduction

Honeydew is a solution of sugars and amino acids produced mainly by sucking insects (Del Claro and Oliveira 1996; Fisher et al. 2002), with aphids in particular excreting copious quantities of honeydew (Dixon 1997). It is the main food of several ant species (Carroll and Janzen 1973; Skinner 1980) and to guarantee their food supply, ants protect aphids against predators and parasitoids (Fritz 1983; Völck 1992), transport them to parts of the plant with better quality sap supply (Way 1963; Collins and Leather 2002), protect their eggs (Pontin 1960; Matsuura and Yashiro 2006), and provide some hygienic services (Nixon 1951). Ant attendance increases the feeding rate (Banks and Nixon 1958; Takeda et al. 1982) and reproduction rate (Stadler and Dixon 1999; Flatt and Weisser 2000) of aphids and delays their dispersion (Kindlmann et al. 2007). However, the ant–aphid association may be costly to aphids (Yao et al. 2000), depending on the size of the aphid colony (Breton and Addicott 1992; Katayama and Suzuki 2002), the strength of ant–aphid interaction (facultative or obligate) (Stadler and Dixon 1999), and the quality of the excreted honeydew (Sakata 1995). It has become apparent that small colonies of tended obligate myrmecophile aphids which produce a higher quality of honeydew are the most prone to increase their abundance under ant attention (Stadler and Dixon 1999; Katayama and Suzuki 2002). As a consequence of the ecological services provided by ants to aphids, and despite the costs, the numbers of some aphid species may increase on plants where they are attended even if they are at low densities (Flatt and Weisser 2000).

Through their collection of honeydew, ants may affect other components of the community (Carroll and Janzen 1973), such as arthropod abundance (Ito and Higashi 1991; James et al. 1999) plant fitness (Rico-Gray and Castro 1996;

Renault et al. 2005), or microorganism activity in litter (Stadler et al. 2005). However, each ant species may have different effects (Itioka and Inoue 1999; Sipura 2002) according to their diet (Mooney and Tillberg 2005), aggressive behavior, and numerical abundance (Gibb and Hochuli 2003). In particular, dominant ant species that collect honeydew monopolize large aggregations of honeydew-producing insects and displace other ant species with similar ecological traits, thus structuring the ant community (Wetterer et al. 1999; Blüthgen et al. 2004). This ecological dominance is particularly evident in the case of invasive ants (Wetterer et al. 1999; Abbott 2005; Cremer et al. 2006). In fact, it has been suggested that a key component of the success of invasive ant species in novel environments is the mutualistic interactions with native honeydew-producing Homoptera (Davidson 1998; Simberloff and Von Holle 1999; Helms and Vinson 2002; Lach 2003). As a consequence, the comparison of honeydew collection between local and invasive ant species with similar ecological traits enables us to contrast the effect of invasive ant species with that of local ants on the same component of the community and to survey the role of novel mutualisms in biological invasions success.

In Catalonia, northeastern Spain, the invasive ant *Lasius neglectus*, Van Loon, Boomsma et Andrásfalvy is displacing the native ant *Lasius grandis*, Forel (Rey and Espadaler, unpublished). Both ant species are monomorphic and tend aphids in many trees and shrubs. However, the native workers are bigger (head length 1.04 vs. 0.80 for the invasive species) and their colonies are monogynous (invasive species are polygynous). *Lasius grandis* is widely distributed in the Iberian Peninsula and nests in open habitats as well as in woodland, but always where there is a certain degree of humidity (Seifert 1992). To date, the invasive ant is distributed in Spain in 17 localities (<http://www.creaf.uab.es/xeg/Lasius/Ingles/distribution.htm>; last access March 2008). The data currently available on *L. neglectus* activity show that this invasive ant has a 24-h activity cycle (<http://www.creaf.uab.es/xeg/Lasius/Ingles/gr2dailyactivity.htm>). At this time, a complete 24-h activity cycle is not available for *L. grandis*, but other *Lasius* (s.str.) ant species also show a 24-h activity period. *Lasius lasioides* in northern Tuscany, Italy (Fig. 1, Santini et al. 2007) was found to show continuous activity between May and July, and in the state of Maryland (USA) *L. alienus* in a woodlot of a second-growth forest composed mostly of oaks (*Quercus* spp.) and Virginia pines (*Pinus virginianus*) also showed an activity period of 24 h (Fig. 3, Feller 1989).

The general aim of this study was to compare food collection of two *Lasius* ant species, one invasive and non-native, *L. neglectus*, and the other a local, native ant, *L. grandis*, that have similar ecological requirements. We performed the study over two activity seasons in an urban

forest invaded by *L. neglectus* where some trees remained occupied by the native ant *L. grandis*. We chose holm oaks visited by one of these ant species. Due to the unicolonial social structure of *L. neglectus*, it was not possible to quantify honeydew collection by nest as is usually done (Jensen 1976; Skinner 1980), so we present the results of honeydew collection per tree. We quantified aphid abundance and estimated ant honeydew collection and honeydew production of the tended aphid species. As honeydew-collecting ants complement their diet with insects (Offenberg 2001), we also estimated the predation rate.

We hypothesized that aphid abundance and honeydew production would increase when *L. neglectus* tended aphids, as this effect has been shown with other invasive ants (Ness and Bronstein 2004), with the consequence that the invasive ant would collect more honeydew than the native ant. Considering that most of the invasive ants fuel their activity by honeydew collection (Holway et al. 2002), we also hypothesized that *L. neglectus* would capture a lower percentage of preys than the native ant *L. grandis*.

Materials and methods

Study site

This study was performed on the campus of the Autonomous University of Barcelona (41°30'N, 2°6'E). The area comprises 264 ha, of which 81 ha are forest fragments of holm oak (*Quercus ilex* L.), mixed forest (*Pinus* sp. plus *Quercus* sp.), and pine forest (*Pinus halepensis* Mill. or *P. pinea* L.). In the first two forest categories, the understorey comprises *Asparagus acutifolius* L., *Crataegus monogyna* Jacq., *Rubia peregrina* L., *Rubus ulmifolius* Schott, *Ruscus aculeatus* L., *Smilax aspera* L., *Viburnum tinus* L., and *Hedera helix* L., while in the more open forest areas, it comprises *Spartium junceum* L., *Juniperus communis* L., and *Rosmarinus officinalis* L. In the pine forest, the understorey is sparse, with *Brachypodium sylvaticum* (Huds.) Beauv. and *Ulex parviflorus* Pourr. Forest edges are bounded by roads or gardened areas where there are some isolated trees and bushes. *Lasius neglectus* was first recorded on the campus in 1997 in a pile of rubble close to one of the railway stations of the University. Nowadays, this ant occupies 15% of the campus area, including forests, shrubland, gardens, and under pavements. In the forest area, between 39 and 100% of the colonized trees (colonized = visited by ants throughout the activity period, May to October) were found to be visited by *L. neglectus* while between 0 and 16% remain visited by the native ant *L. grandis*.

The climate is Mediterranean, with a wet spring and autumn and a dry winter and summer. Mean annual temperature is 16.5°C and mean annual rainfall is 575 mm.

Tree selection

In May 2003, we chose 12 *Quercus ilex* trees in the area occupied by *L. neglectus*; six of these trees were colonized by *L. neglectus*. We chose those holm oaks that we knew from previous observations were visited by foraging workers during the activity period. The other six *Quercus ilex* were visited by *L. grandis* in May, but we did not have any previous information on ant visitation of those trees, and by June two of them had been abandoned by *L. grandis*. We continued observing those trees that remained colonized during the activity period of *L. grandis* in 2003. In May 2004, we chose six *Q. ilex* visited by *L. grandis* but again, after 1 month, one was definitely abandoned. During the ant activity period, tree visitation changed, and in some of the chosen holm oaks workers' activity ceased suddenly and reappeared later. When we found no activity in a particular tree, we considered honeydew collection and insect predation to be zero. Trees visited by *L. neglectus* had a greater diameter (diameter at breast height, DBH) than those visited by *L. grandis* [DBH (mean \pm SE) *L. neglectus* 33.06 \pm 3.39 cm, $n = 6$; *L. grandis* 20.50 \pm 3.70 cm, $n = 5$; t test, $t = 2.50$, $P = 0.034$]. The distance between chosen trees was 107.25 \pm 42.26 m (mean \pm SE) with a range of 1–527.38 m.

Ants may adjust honeydew collection according to the distance from the nest, the quantity of the resource, and the risk of being preyed upon (Dreisig 1988; Wright et al. 2000; Mailleux et al. 2003). In our study case, soil entrances from which workers of both ant species climbed the trunks to collect honeydew were at the base of the chosen trees, and the area of canopy where ants search for aphids did not differ [canopy area (mean \pm SE) *L. neglectus* 50.24 \pm 9.31 m²; *L. grandis* 27.20 \pm 10.20 m²; $F_{1,9} = 2.79$, $P = 0.129$]. We therefore assume that honeydew collection was not influenced by distance (Wright et al. 2000; Nonacs 2002).

Honeydew collection and production

Honeydew collection by *L. neglectus* was estimated in both years, but for *L. grandis*, we consider we have reliable data only for 2004. In 2003, several trees were abandoned by *L. grandis* (see tree selection). From May to October, we estimated collected honeydew per tree by subtracting the weight of filled workers from the weight of empty workers (Herzig 1937). In 2003, we estimated collected honeydew every 18 days, while in 2004 we carried out the measurements every 25 days. Four samplings were carried out on

each sample day: at 0600, 1100, 1700, and 2300 hours. These sampling hours were chosen because they represent moments of the days at which it was expected that the temperature varies significantly. Temperature variations influence ant activity as well as honeydew production (Mittler 1958; Degen and Gersani 1989; Hölldobler and Wilson 1990; Dungan and Kelly 2003). We first recorded workers' activity on the trunk over a 2-min period of each sampling hour; workers' activity was considered to be the number of workers in a trunk trail crossing an imaginary line. We then collected the up-going ants (empty ants) and the returning ants (honeydew-loaded ants) from the tree trunks. In the case of *L. neglectus*, we collected at least 30 workers per group, while from trees visited by *L. grandis*, we sampled 15 workers. Ants were immediately weighed in the laboratory (empty and loaded ants) and counted and the mean weight per ant of empty and loaded ants, respectively, estimated. The difference between these means represents the amount of honeydew collected per ant. By multiplying this amount by the workers' activity in a 1-min period, we obtained a collection rate (collected honeydew \times min⁻¹). Ants were weighed using a Precisa 250 A microbalance with a precision of 0.0001 g.

From each sampling hour (0600, 1100, 1700, and 2300 hours), we extrapolated the amount of honeydew collected per minute on each tree to an hour. To calculate collected honeydew per day for each tree, we multiplied the amount of honeydew collected per hour for the hours between two consecutive sampling hours. We then summed these four values and obtained the total quantity of collected honeydew per day for each tree. Finally, we extrapolated the result of these calculations for 1 day to 1 month. The mean of all sampled trees represents the amount of honeydew collected per month and per tree and is the value reported Table 1. The sum of all months represents the total amount of honeydew collected per tree during the ant activity period.

We are aware that our estimation of collected honeydew per tree and per month depends on an 8-min observation period of ant activity and that this sampling scheme may not have captured all of the complete details of ant activity patterns. However, between May and October trees were visited between 1000 and 1800 hours on different days to perform other samplings and estimations (aphid counting, arthropods samplings, leaves samplings). During these samplings we never noticed that *L. neglectus* or *L. grandis* showed a peak of activity that could be interpreted as a different response to external factors, such as temperature.

Lachnus roboris was the main tended aphid in the surveyed holm oaks. To estimate *Lachnus* honeydew production (microliters of honeydew per aphid per hour), we chose (July 2006) three tended colonies of a similar number of aphids and developmental stage from eight holm

Table 1 Amount of honeydew collected per tree, workers' activity per minute and tree, and amount of honeydew collected per ant at holm oaks visited by *Lasius neglectus* or by *L. grandis*

Ant activity period	<i>Lasius neglectus</i>			<i>Lasius grandis</i>		
	Honeydew (kg/T)	Ant activity (ant/min T)	Honeydew (mg/ant)	Honeydew (kg/T)	Ant activity (ant/min T)	Honeydew (mg/ant)
May	0.50 ± 0.13	58.66 ± 9.19	0.153 ± 0.022	0.14 ± 0.14	9.29 ± 10.08	0.365 ± 0.073
June	0.38 ± 0.13	127.32 ± 32.37	0.122 ± 0.024	0.25 ± 0.14	22.33 ± 35.45	0.278 ± 0.029
July	0.82 ± 0.18	281.23 ± 96.02	0.127 ± 0.027	0.33 ± 0.20	20.73 ± 105.18	0.399 ± 0.055
August	0.20 ± 0.06	53.17 ± 18.05	0.141 ± 0.033	0.06 ± 0.07	7.40 ± 19.77	0.210 ± 0.019
September	0.14 ± 0.06	45.35 ± 9.00	0.096 ± 0.028	0.02 ± 0.07	1.64 ± 9.86	0.370 ^a
October	0.05 ± 0.03	15.77 ± 5.79	0.183 ± 0.084	0.02 ± 0.03	3.09 ± 6.48	0.335 ± 0.042

Values are given as the mean ± standard error (SE)

See text for specific differences between ant species

^a In September, there was activity at only one holm oak visited by *L. grandis* so the standard error SE could be not computed for milligrams of honeydew per ant

oaks, four visited by each ant species, *L. neglectus* or *L. grandis*. We chose one or two aphids per colony, in different stages, and during a 40-min period we counted the number of drops excreted while they were tended by ants. According to Fisher et al. (2002), honeydew produced by young larvae can be distinguished from that produced by older larvae plus adults. Using this criterion, we distinguished three classes of developmental stages: young larvae (larvae from the first and second stage), old larvae (larvae from the third and fourth stage), and adults (apterous and winged). All trees were inspected on two consecutive days between 0900 and 1200 hours. An attempt to directly estimate the volume of drops by collecting them with a micropipette failed. Tending ants were much quicker than us at capturing the drop or they stole the drop when it was entering the micropipette. We refrained from excluding ants because drop volume changes when ants are not present (Yao and Akimoto 2001), and this change occurs within a few minutes (Mittler 1958).

Insect predation

In 2004, we counted workers' activity on the chosen holm oaks during a 3-min period at intervals of 20 days. Immediately thereafter, during a 3-min period we sampled all of the workers that carried items in their mandibles. At the laboratory we identified the items with an Olympus SZ30 stereoscopic microscope. All samplings were performed in the morning.

Aphid abundance

For accessibility reasons, we limited our search to the lower half of the tree crown. Consequently, from the previously

chosen holm oaks, we were forced to exchange two trees occupied by *L. neglectus* and one tree occupied by *L. grandis* for new ones with an adequate number of low branches. The DBH of the new holm oaks did not differ (*L. neglectus* 30.45 ± 2.92 cm, $n = 6$; *L. grandis* 25.92 ± 3.15 cm, $n = 5$; t test, $t = 1.05$, $P = 0.314$). In both years, we examined all terminal twigs up to a height of 4.25 at 25-day intervals. The mean time we counted aphids was 51 ± 7 min ($n = 31$) at *L. neglectus* trees and 45 ± 7 min ($n = 26$) at *L. grandis* trees (t test, $t = 0.65$, $P = 0.522$). The number of observed twigs varied greatly between trees depending on the crown size, accessibility, and month (*L. neglectus* trees 170–1841 twigs per tree; *L. grandis* trees 88–1015 twigs per tree; t test, $t = 1.43$, $P = 0.156$).

At each tree, we recorded aphid abundance and the number of infested twigs. We distinguished between aphids grouped or not grouped in a colony, and between tended and not tended aphids (only in 2004). We considered a colony to be a group of five or more aphids (Michel 1942; Katayama and Suzuki 2002) and that a twig was infested when at least one aphid was feeding on it. We considered a colony to be tended when there was at least one worker ant actively touching the back of the aphids with their antennae. The number of tending ants was counted in tended colonies. To estimate ant attendance, we followed Fisher et al. (2002) who proposed quantifying the intensity of ant-attendance as a numerical relation between the number of tending ants and the size of the aphid colony. As the body size of the two ant species studied here differs, we recalculated this index as the relation of biomasses (Paris 2005). For the ant species, we considered the average weight of empty ants (median ± SE, *L. neglectus* 0.822 ± 0.006 mg, $n = 132$; *L. grandis* 1.431 ± 0.038 mg, $n = 86$) obtained during the estimation of honeydew collection. For aphids, we weighed ovipares from the same colony (4.52 ± 0.00018 mg, $n = 20$).

Statistical analysis

For holm oaks, tree diameter (DBH) is a good indicator of crown size (Canadell et al. 1988), which is in turn related to the aphid carrying capacity of a tree (Dixon 1997) and hence to the amount of honeydew that the ants would be able to collect. As the trees visited by *L. neglectus* had a significantly greater diameter (see **Tree selection**), we tested the correlation between tree diameter and the total amount of honeydew collected per tree during the ant activity period. As no significant relation was found between these variables for either ant species (*L. neglectus* $r^2 = 0.04$, $P = 0.53$; *L. grandis* $r^2 = 0.70$, $P = 0.07$), we analyzed honeydew collection, per tree and per worker of each ant species (per ant), and ant activity with a repeated measures analysis of variance (ANOVA), with ant species as a fixed factor. The comparison between years of collected honeydew per tree by *L. neglectus* was analyzed with repeated measures ANOVA considering year as a factor. Honeydew production and the frequency of drop excretion (frequency \times drop volume) were compared using a two-way ANOVA, with ant species and aphid developmental stage as fixed factors.

For each tree, we averaged aphid abundance, the percentage of infested twigs, and the percentage of aphids grouped in colonies or alone. Aphid abundance was analyzed with an analysis of covariance (ANCOVA) where ant species and year were considered to be fixed factors and the number of observed twigs to be the covariate. We used this statistical analysis because we did not survey in all months nor did we survey the same number of twigs on all trees. The percentage of infested twigs and the percentage of aphids grouped in colonies or alone were analyzed with an ANOVA. We considered ant species and year as fixed factors for the first analysis and ant species, year, and grouping factor as fixed factors for the second analysis. The percentage of untended aphids and the intensity of ant-attendance were analyzed with an ANOVA considering ant species as the factor. Year was not included as a factor because these variables were estimated only in 2004.

Finally, the percentage of workers carrying prey was analyzed with an ANOVA, with ant species as the fixed factor. Tukey post hoc comparisons were run when significant differences were found ($P < 0.05$).

Abundance variables were transformed by the expression $x' = \sqrt{(x + 1)}$ to attain normality, and percentages were arcsin transformed $x' = \text{Arc sin}(\sqrt{x}/100)$. All analysis was performed using Statistica 6.0 (Statsoft 2001). The results are given as mean \pm standard error.

Results

Honeydew collection by ants

The invasive ant *L. neglectus* collected significantly less honeydew on a per-tree and a per-month basis in 2003 than in 2004 (2003: 0.130 ± 0.023 kg; 2004: 0.348 ± 0.068 kg; ANOVA, $F_{1, 10} = 7.13$, $P = 0.024$). *Lasius neglectus* showed a different phenology of honeydew collection between years (year \times month, ANOVA, $F_{5, 50} = 3.27$, $P = 0.012$). Post hoc comparisons showed that in both years most of the honeydew was collected during the first 3 months of the ant activity period (Tukey, $P < 0.001$), but in 2003, honeydew collection peaked at the end of the ant activity period (October), while in 2004 it achieved the lowest values at this time.

In 2004, *L. neglectus* collected 2.09 kg (range 0.55–3.54 kg/tree) during the whole activity period while *L. grandis* collected 0.82 kg (range 0.37–1.60 kg/tree). Comparisons between the native and the invasive ant showed that the invasive ant *L. neglectus* collected significantly more honeydew per tree than the native ant *L. grandis* (*L. neglectus* 0.348 ± 0.066 kg; *L. grandis* 0.136 ± 0.034 kg) (Tables 1, 2). Both ant species showed a similar phenology of honeydew collection (Tables 1, 2), with honeydew collection peaking significantly in July (Table 2) (Tukey, $P < 0.05$). *Lasius neglectus* was ninefold more active than *L. grandis* (ants per minute, mean \pm SE, *L. neglectus* 96.92 ± 26.20 ants; *L. grandis* 10.74 ± 2.35 ants) (Tables 1, 2), although

Table 2 Results of the repeated measures ANOVA of collected honeydew per tree, workers activity per minute and per tree and amount of honeydew collected from holm oaks visited by *L. neglectus* or by *L. grandis* in 2004

Source of variation	Honeydew (kg/T)			Ant activity (ant/min T)			Honeydew (mg/ant)		
	df	F	P	df	F	P	df	F	P
Ant species (A)	1	5.71	0.41	1	5.94	0.038*	1	12.70	0.016*
Month (M)	5	7.23	<0.001*	5	3.38	0.011*	3	2.65	0.086
A \times M	5	1.37	0.254	5	2.52	0.043*	3	1.64	0.223

* Significant values ($P < 0.05$) determined by ANOVA (analysis of variance)

September and October were not included in the analysis of collected honeydew per ant due the lack of enough replicates of holm oaks visited by *L. grandis*

both ant species showed activity at all of the surveyed times (0600, 1100, 1700, and 2300 hours). The invasive ant carried significantly less honeydew per ant than the native ant (honeydew per ant, *L. neglectus* 0.144 ± 0.029 mg; *L. grandis* 0.304 ± 0.034 mg) (Tables 1, 2). Carried load did not vary among months (Table 2).

Detailed tables of the collected honeydew per tree of both years and for both ant species are provided in Appendix.

Honeydew production by aphids

The surveyed aphid colonies were of a similar size (*L. neglectus* 6.62 ± 0.62 aphids per colony; *L. grandis* 6.66 ± 0.66 aphids per colony; ANOVA, $F_{1, 22} = 0.088$, $P = 0.770$, $n = 24$ colonies) and a similar composition (aphid stage per colony \times ant species; young larvae: *L. neglectus* 4.00 ± 0.55 , *L. grandis* 3.58 ± 0.66 ; old larvae: *L. neglectus* 0.75 ± 0.35 , *L. grandis* 1.33 ± 0.41 ; adults: *L. neglectus* 2.17 ± 0.58 , *L. grandis* 1.75 ± 0.49 ; ANOVA, $F_{2, 66} = 1.03$, $P = 0.362$).

For a given tree, we averaged the data of the three colonies per developmental stage. Excretion frequency (drops per hour and per aphid) was significantly higher when *Lachnus* was tended by the invasive ant (drops per hour and per aphid, *L. neglectus* 19.08 ± 2.54 ; *L. grandis* 10.80 ± 2.31 ; ANOVA, $F_{1, 15} = 4.93$, $P = 0.042$). Different developmental stages showed a similar excretion frequency (drops per hour and per aphid, young larvae 15.69 ± 3.37 , old larvae 17.57 ± 3.16 , adult 12.36 ± 2.92 ; ANOVA, $F_{2, 15} = 0.55$, $P = 0.588$). The attention of *L. neglectus* did not modify the excretion frequency of any particular aphid developmental stage (ant species \times aphid stage, ANOVA, $F_{2, 15} = 0.77$, $P = 0.473$).

Aphid abundance

We recorded two aphid species, *Hoplocallis picta* and *Lachnus roboris*. The aphid *H. picta* was rarely tended by the ant species and was not found on all sampling dates (only in May and occasionally in July or August), so the variables considered for aphids were analyzed only for *Lachnus*.

In both years, mean aphid abundance per tree and the percentage of infested twigs did not differ between trees colonized by the invasive or the native ant (tree types hereafter) (aphid abundance per tree, *L. neglectus* 59.43 ± 16.90 , *L. grandis* 28.54 ± 11.92 ; % infested twigs, *L. neglectus* $2.75 \pm 0.91\%$, *L. grandis* $1.37 \pm 0.63\%$) (Table 3). Given the high number of twigs surveyed (see Materials and methods), this result underlines the scarcity of *Lachnus* in *Quercus ilex*. The abundance of *Lachnus* per tree

Table 3 Results of ANCOVA of aphid abundance (covariate = number of observed twigs) and ANOVA analysis of percentage of infested twigs

Source of variation	Aphid abundance			Infested twigs (%)		
	df	F	P	df	F	P
Ant species (A)	1	3.62	0.071	1	3.08	0.094
Year (Y)	1	21.90	<0.001*	1	6.27	<0.001*
A \times Y	1	1.53	0.230	1	1.32	0.263

* Significant values ($P < 0.05$)

ANCOVA, Analysis of covariance

Ant species and year were included as fixed factors

and the percentage of infested twigs were significantly greater in 2004 than in 2003 (aphid abundance, 2003: 11.15 ± 2.8 , 2004: 79.39 ± 16.74 ; % infested twigs, 2003: $0.052 \pm 0.018\%$, 2004: $4.176 \pm 0.785\%$) (Table 3). In 2004, the increase in *Lachnus* abundance occurred independently of which ant species tended the aphid (Fig. 1a and b; Table 3).

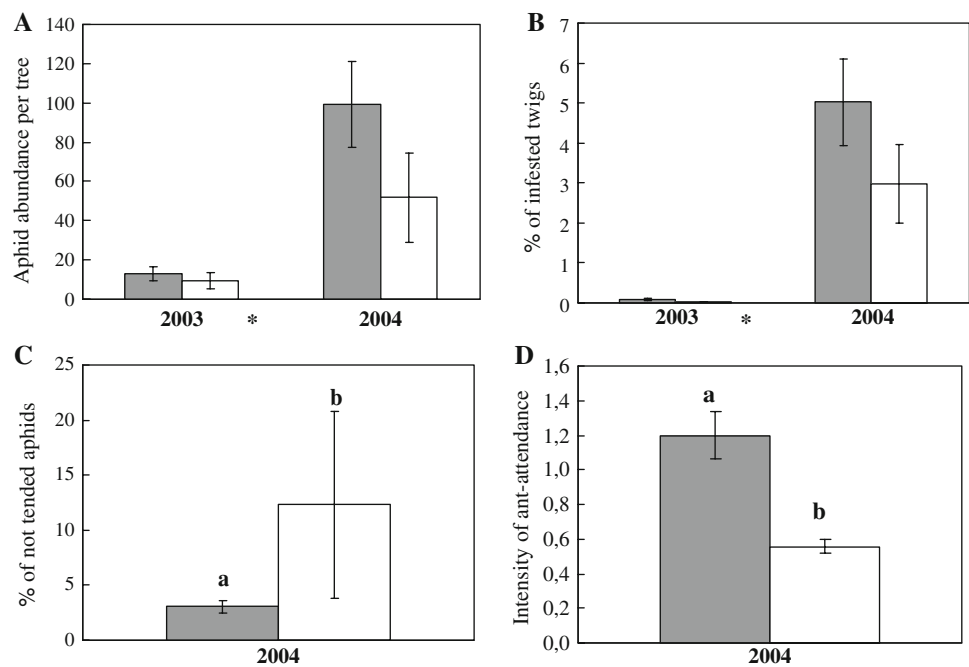
In 2003, the percentage of aphids grouped in colonies (= more than five aphids in the same twig) was significantly lower than that of aphids alone (year \times grouping, aphids in colonies $26.8 \pm 9.7\%$, aphids alone $64.9 \pm 11.1\%$; ANOVA, $F_{1, 40} = 7.65$, $P = 0.009$; Tukey, $P = 0.012$). However, in 2004, when aphid abundance increased significantly (see above), the percentages of aphids in colonies or alone were similar (ant species \times grouping, ANOVA, $F_{1, 40} = 3.35$, $P = 0.075$). Additionally, the percentage of not tended aphids was fourfold lower in the holm oaks colonized by *L. neglectus* than in those colonized by *L. grandis*, although the difference was not significant due to the very high variation in *L. grandis* data (ANOVA, $F_{1, 10} = 1.17$, $P = 0.304$ (Fig. 1c).

The intensity of ant-attendance by the invasive ant *L. neglectus* was significantly higher than that of the native ant *L. grandis*. We reached at the same result using indices based on a numeric relation (Fig. 1d) (ANOVA, $F_{1, 8} = 5.67$, $P = 0.044$) or biomass relation between ant and aphids (ANOVA, $F_{1, 8} = 9.97$, $P = 0.014$).

Insect predation

Relative to *L. neglectus* workers (invasive ant), a significantly higher percentage of *L. grandis* workers (native ant) carried items (insects, part of insects, and unidentified items) (mean \pm SE, *L. grandis* $9.91 \pm 2.62\%$, *L. neglectus* $3.48 \pm 0.67\%$; ANOVA, $F_{1, 54} = 7.10$, $P = 0.011$). The main prey insects of both ant species were Psocoptera (*L. grandis* 33.8%, *L. neglectus* 31.1%) and the aphid *Hoplocallis picta* (*L. grandis* 35.4%; *L. neglectus* 37.8%).

Fig. 1 Mean \pm SE of aphid abundance (a), percentage of infested twigs (b), percentage of not tended aphids (c), and intensity of ant attention (d) at holm oaks occupied by the invasive ant *Lasius neglectus* (shaded) or by the native ant *Lasius grandis* (open). Asterisk indicates significance between years. Means with different letters differ significantly ($P < 0.05$) between ant species. a, b There were no significant differences between ant species



Discussion

Honeydew collection by ants varies considerably between ant species. It has been estimated at 230 kg per season (May–September) and per nest of *Formica rufa* (Skinner 1980), at 15 kg per season (March–May) and per nest of *Polyrhachis simplex* (Degen and Gersani 1989), and at 2.37 kg per year and per nest of *Formica pratensis* (Jensen 1976). All of these values are dry weight estimates and were calculated per nest. Nest densities of five and 0.1 nests per hectare have been reported for *Formica rufa* (Fowles 1994) and *F. pratensis* (Holec and Frouz 2005), respectively, implying 1150 kg dry weight/ha and per season for *F. rufa* and 0.24 kg dry weight/ha and per year for *F. pratensis*. Our results showed that the invasive ant *L. neglectus* collected 2.09 kg fresh matter per tree. Other research also carried out at this same urban forest showed that between 1 and 27 holm oaks were colonized during the activity period (May–October). Assuming that our results represent the mean collected honeydew per tree, the invasive ant *L. neglectus* can be considered to have collected 87.44 kg fresh weight per hectare and per season from holm oaks. With 84% of honeydew consisting of water (Auclair 1963), the honeydew collected by the invasive ant is equivalent to 13.99 kg dry weight per hectare and per season. Although holm oaks are the most common tree in the studied forest, there are also pines, other oaks species, and elms from which *L. neglectus* can collect honeydew (Paris 2005). This means that on a per-hectare basis, the invasive ant may actually collect a higher quantity of honeydew than our estimation. *Lasius neglectus* may also

collect 2.55-fold more honeydew from holm oaks than the native ant *L. grandis*. In non-invaded forests from the study area, *L. grandis* is the most common ant climbing holm oaks, possibly collecting 9.50 kg dry weight per hectare and per season (47% less than *L. neglectus*). As there are other local ants that collect honeydew from holm oaks in the study area, one question remaining to be answered is whether honeydew collected from holm oaks per hectare and per season by the whole native ant community may reach a quantity similar to that estimated for *L. neglectus* alone.

A combination of four variables may be determining factors in the higher honeydew collection of *L. neglectus*. First, the higher activity of the invasive ant relative to the native may have increased the probability of finding aphids in the canopy. Second, *Lachnus* was 2.11-fold more abundant in holm oaks colonized by *L. neglectus*; however, this variable should be interpreted with caution because there was no significant difference, just a tendency. Third, the rate of *Lachnus* honeydew production per hour and per aphid doubled when they were tended by the invasive ant. Finally, the feeding preferences of each *Lasius* species differs. Each of these variables and their relation to honeydew collection is discussed in detail in the following paragraphs.

The numerical and behavioral dominance (ecological dominance sensu Davidson 1998) of invasive ants has already been proposed as one mechanism by which these ants exploit trophobionts more efficiently than native ants (Holway et al. 2002). In this study, the abundance of *L. neglectus* workers foraging on trunk trails was ninefold

higher than that of the native ant *L. grandis*, reaching 12-fold on some days when aphid samplings were performed. The higher activity of *L. neglectus* on holm oaks should result in a higher rate of aphid discovery, thereby allowing the invasive ant to collect more honeydew per tree despite their smaller body size (which implies a smaller loading capacity) relative to *L. grandis*. Additionally, Cremer et al. (2006) reported that *L. neglectus* is highly aggressive towards the three native *Lasius* species, especially *L. grandis*, implying that if aphid colonies are discovered quickly by *L. neglectus*, they remain under its control. The lower percentage of unattended *Lachnus* in trees colonized by the invasive ant compared to trees colonized by the native ant supports this concept.

The abundance of *Lachnus roboris* and the percentage of twigs infested by this aphid suggest that it is rare in urban holm oaks. This observation was also made during a 3-year study in urban trees from the streets and parks of Lleida (northeastern Spain) where *Lachnus* was found on only one occasion in one holm oak (Pons, personal communication) and in holm oak forests from Cordoba (southern Spain) where this aphid species appeared in 10% of the samples (Melia et al. 1993). It would appear that the occurrence of *Lachnus roboris* is rare in Mediterranean forests compared with the situation in temperate forests, where this aphid species is more frequent (Sudd and Sudd 1985). It is not clear if the invasive ant promotes the higher abundance of *Lachnus roboris* or if foragers search for those trees with more aphids. Both could be the case. Only an experiment that manipulates the abundance of aphids, tending ants, and aphid predators could clarify this aspect. We have attempted to perform this type of experiment in the laboratory and in the field, but the colonies of *Lachnus roboris* growing on *Quercus ilex* saplings did not live more than 2 weeks, which was too short a time to achieve a reliable result in that the saplings had not yet produced acorns, and previous observations had shown that *Lachnus roboris* feeds most of the time on acorn petiole or acorn cap (Paris 2005).

When *Lachnus* was tended by *L. neglectus* their excretion rate (number of drops per hour and per aphid) increased by 77% and honeydew production per hour and per aphid doubled compared to the effect of tending by *L. grandis*. Yao and Akimoto (2001) found that *Tuberolachnus quercicola* increase their excretion rate by 87% when tended by *Formica yessensis* compared to when not tended. Previous studies on *Aphis fabae* (Banks and Nixon 1958), *Tuberolachnus salignus* (Mittler 1958), and *Aphis craccivora* (Takeda et al. 1982) confirm that aphids increase their excretion frequency when they are tended by ants. In our study, we compared two *Lasius* species instead of comparing ants' absence–presence, as was done in these earlier studies. Our results suggest that a change in ant identity can increase aphid excretion frequency in a similar

proportion as a change in ant presence (from no ants to ant presence). However, it is still debatable if the tending of *L. neglectus* actually changed the production of honeydew by *Lachnus*. According to Yao and Akimoto (2001), aphids always feed at their optimal rate and alter their excretion frequency and drop volume according to ant demands—but they do not change their total honeydew production (excretion frequency \times drop volume). Honeydew production by aphids is also affected by plant quality and its phenology (Cushman 1991). We believe that the differences observed were truly due to ant species tending and not to the fact that aphids fed on a superior qualitative tree. We analyzed the nitrogen content of leaves as a measure of plant quality and found no difference in the quality of the leaves of holm oaks colonized by *L. neglectus* (mean \pm SD, $1.67 \pm 0.36\%$) or *L. grandis* ($1.33 \pm 0.17\%$). One mechanism by which *L. neglectus* raised honeydew production could be the higher intensity of ant-attendance. In this study we applied numeric and biomass relations between tending ants and aphid colony size to develop an index of ant-attendance. Based on the results of this analysis, we suggest that the intensity of ant-attendance can also be estimated as a relation between the number of contacts by tending ants and aphid colony size because it is by antennal contact that ants stimulate aphid excretion behavior (Wool et al. 2006).

Among honeydew collecting ants, the percentage of workers carrying insects may vary from 2% for *Crematogaster matsumurai* (Harada 2005) to 10% for *Formica pratensis* (Jensen 1976) and up to 36% for *Formica rufa* (Skinner 1980). Our estimation showed that 9.91% of the workers of the native ant *L. grandis* carried insects in comparison to 3.48% of the workers of the invasive ant *L. neglectus*, suggesting that the native ant is more predacious. This may explain in part the lower honeydew collection of the native species. However, Cannon and Fell (2002) reported that fewer than 1% of foragers of *Camponotus pennsylvanicus* returned to the nest with visible solid food in their mandibles although crop-borne nitrogenous food made up nearly half of all food retrieved by foragers. Apparently many ant species transport liquids from prey internally, consuming the insects where they are found (Ayre 1959). Considering the higher abundance of workers and queens in the supercolonies of *L. neglectus* (Espadaler et al. 2004), honeydew may subsidize foraging, but nitrogen is needed to feed larvae and sexual forms. A more accurate estimation of nitrogen intake by this invasive ant is therefore needed.

Conclusion

We conclude that in the study area the ecological dominance of the invasive ant *L. neglectus* allowed workers to

monopolize a greater number of *Lachnus* colonies, which in turn increased the honeydew production of these aphid colonies when tended by *L. neglectus*. As a result, the invasive ant collected more honeydew and was able to subsidize its higher activity.

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Appendix

Table 4 Total kilograms of collected honeydew per tree per month during the ant activity period in 2003 for *Lasius neglectus* and in 2004 for *L. neglectus* and *L. grandis*

<i>Lasius neglectus</i> –2003	Tree number					
	1	2 ^a	3	4 ^a	5	6
May	0.238	0.213	0.171	0.000	0.197	0.000
June	0.466	0.000	0.210	0.000	0.287	0.251
July	0.567	0.279	0.074	0.089	0.066	0.124
August	0.100	0.059	0.000	0.063	0.081	0.213
September	0.105	0.002	0.000	0.044	0.046	0.050
October	0.383	0.015	0.073	0.050	0.099	0.078
Total Hd (kg) per tree	1.859	0.569	0.528	0.246	0.776	0.716
<i>Lasius neglectus</i> –2004	Tree number					
	1	2 ^a	3 ^a	4 ^a	5 ^a	6
May	0.299	0.619	0.201	1.208	0.570	0.110
June	0.140	0.690	0.470	0.064	0.892	0.000
July	0.665	1.497	0.631	0.771	1.379	0.000
August	0.274	0.000	0.000	0.140	0.498	0.269
September	0.508	0.000	0.005	0.042	0.175	0.140
October	0.221	0.000	0.000	0.000	0.025	0.029
Total Hd (kg) per tree	2.108	2.806	1.307	2.225	3.540	0.548
<i>Lasius grandis</i> –2004	Tree number					
	1 ^a	2 ^a	3 ^a	4 ^a	5	
May	0.326	0.270	0.000	0.085	0.033	
June	0.140	0.562	0.363	0.108	0.052	
July	0.525	0.650	0.234	0.000	0.238	
August	0.170	0.064	0.000	0.000	0.050	
September	0.000	0.000	0.116	0.000	0.000	
October	0.031	0.049	0.015	0.000	0.000	
Total Hd (kg) per tree	1.192	1.595	0.728	0.194	0.372	

^a Trees that were also used to estimate aphid abundance

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