POPULATION ECOLOGY

Habitat-related microgeographic variation of worker size and colony size in the ant *Cataglyphis cursor*

Johanna Clémencet · Claudie Doums

Abstract In social insects, colony size is a crucial life-history trait thought to have major implications for the evolution of social complexity, especially in relation to worker size polymorphism. Yet, little is known about how ecological factors can affect and constrain colony. Here, we explored the pattern of colony-size and worker-size variation in the Mediterranean ant *Cataglyphis cursor*, in relation to the type of habitats colonized (seaside vs. vineyard). The high level of the water table in the seaside habitat could constrain the depth of *C. cursor* underground nests and directly constrain its colony size. If worker size increases with colony size, as observed in other ant species, larger colony size and larger workers should be found in the vineyard populations. By comparing worker size among 16 populations, we verified that workers were significantly larger in the vineyard populations. We further determined that the morphological similarities detected among populations from the same habitat type were not due to geographic or genetic proximity. In two populations from each habitat type, the depth of nests was positively correlated with colony size and colony size with worker size. Using a type II regression approach, we further showed that the difference between the two populations in the depth of nest was sufficient to explain the difference in colony size, and similarly, variation in colony size was sufficient to explain variation in worker size. Our results suggest

that a single proximate ecological factor could lead to significant variation in major life-history parameters.

Introduction

Individual size in insects, as in other organisms, is often considered an important life-history trait that correlates with major fitness parameters such as fecundity, dispersal, mating success or survival (Stearns 1992). In holometabolous insects, the absence of growth during the adult stage prevents any size adjustment after metamorphosis (Nijhout 2003). Adult size is then a fixed parameter determined by genetic and environmental factors acting during the post-embryologic development of the insect and is tightly linked to the development time and growth rate (Nylin and Gotthard 1998). Natural variation in body size has often been investigated at a macrogeographical scale, often in relation to latitude, with the aim of testing Bergmann's rule (Blanckenhorn and Demont 2004 for review). In social insects, variation in individual size has received a lot of attention as it is linked to a key social parameter, the division of labor among colony members (Oster and Wilson 1978; Hölldobler and Wilson 1990). The reproductive individual, the queen, is generally larger than workers, and in *Carebara vidua* can even exhibit thorax volume up to 8,000 times larger than the workers (M. Molet, personal communication).

Even though the workers usually do not reproduce, their body size is still an important life-history trait that can affect the ability of a colony to rear offspring and

J. Clémencet (✉) · C. Doums
Laboratoire Fonctionnement et Evolution des Systèmes
Ecologiques, UMR 7625, Université Pierre et Marie Curie,
Bat A, 7ème étage, CC 237, 7 quai Saint-Bernard,
75252 Paris Cedex 05, France
e-mail: johanna.clemencet@snv.jussieu.fr

therefore impact their indirect fitness. For various ant species, larger workers perform better than smaller workers at carrying out particular tasks linked to foraging and nest defense (Cerdá and Retana 1997; Reyes-Lopez and Fernandez-Haeger 2001; Braendle et al. 2003; Nowbahari et al. 1999, 2000). Such a pattern has also been observed at the interspecific level (Davidson et al. 2004; Ness et al. 2004). Larger workers also tend to survive better (Porter and Tschinkel 1985; Calabi and Porter 1989) and be more resistant to starvation (Heinze et al. 2003). Producing larger workers could therefore be advantageous for the colony. Large workers however are more energetically expensive to manufacture and maintain than small workers, and colonies have to face the traditional trade-off between worker number and size (Backus 1993; Bourke and Franks 1995).

Considering the extra-dimensional level of the colony is therefore necessary for understanding the proximate and ultimate factors determining worker size. Colony can be considered as a super-organism with modular growth similar to certain plants or corals, the modules being the different members composing the colony (Hölldobler and Wilson 1990; Kaspari 2005). Colony size is then determined by the rate of birth and death of its modules. Similarly to worker size, colony size can then be considered as a crucial life-history trait of the super-organism. Colony size is generally positively correlated to colony reproductive success (Oster and Wilson 1978; Tschinkel 1993; Sorvari and Hakkaraien 2005), with only large colonies able to obtain the resources needed to rear the sexuals (Oster and Wilson 1978; Hölldobler and Wilson 1990; Bourke and Franks 1995).

Interestingly, a positive relationship between colony size and worker size has been frequently documented (see Brian 1957; Elmes 1974; Wood and Tschinkel 1981; Porter and Tschinkel 1985; Gibson 1989; Tschinkel 1988, 1993, 1998; Wetterer 1994; Kaspari and Byrne 1995) suggesting that only large colonies can afford the production of large workers. Even though worker size and colony size are two major life-history traits, few studies have investigated their pattern of natural variation among colonies and populations. This is however a crucial step not only for understanding the evolution of life-history traits in social insects, an area still largely unexplored (Bourke and Frank 1995), but also for understanding the evolution of social complexity such as the evolution of worker castes (Hölldobler and Wilson 1990; Fjerdingstad and Crozier 2006) or the reproductive division of labor (Bourke 1999).

In ants, the size of the nesting cavity, and the nature and the availability of nest-building materials are known to potentially constrain colony growth and size (Wilson 1959; Hansell 1987). The Mediterranean ant, *Cataglyphis cursor*, is an interesting species to investigate how a simple proximate ecological factor, the level of the water table, can constrain colony size and indirectly worker size. *C. cursor* nests are underground and possess a single entrance open on a vertical well leading to chambers located up to 1 m deep. Horizontal galleries have never been observed and the volume of nest can only be increased by increasing nest depth (Cagniant 1976; Lenoir et al. 1988; A. Lenoir, personal observation). The depth of the water table is a simple ecological factor that clearly limits the depth of nests (Cagniant 1976; Lenoir et al. 1988). Interestingly, *C. cursor* colonizes two main types of habitat that clearly differ in the depths of their water tables: from 60 cm at the seaside (sandy soil) to 1.20 m in the vineyard (chalky soil; Lenoir et al. 1988).

In this study, we explored the pattern of worker size and colony size variation in *C. cursor* in relation to the type of habitats. *C. cursor* is a monogynous species with dependent colony foundation, the queen founds a new colony with the help of workers (Lenoir et al. 1988). Even if colonies therefore never pass through the critical phase of small incipient colonies, large variation in colony size can still be observed in the field (from 150 to 2,500 workers; Lenoir et al. 1988; A. Lenoir, personal observation).

If the two hypotheses about positive correlations between nest depth and colony size, and between colony size and worker size, are correct in *C. cursor*, we would expect larger colony size and larger workers in the vineyard populations. This prediction was supported by comparing the mean worker size between populations from both types of habitats. Moreover, in two populations (seaside and vineyard), the depth of nests was positively correlated with colony size, and colony size with worker size. Using a type II regression approach, we showed that the difference in the depth of nest between the two populations was sufficient to explain the difference in colony size, and similarly that variation in colony size was sufficient to explain variation in worker size. This suggests that a single proximate ecological factor could lead to significant variation in major life history parameters.

Materials and methods

Variation in worker size among populations

We used workers sampled for a previous population genetic structure study (Clémencet et al. 2005) for which the two types of habitats (five seaside and 11 vineyard populations) were represented. In July 2001, a total of

317 colonies were sampled in these 16 populations (300 × 150 m areas), in Languedoc-Roussillon, France (see Clémencet et al. 2005, for the map of populations). As for the genetic study, only one randomly chosen individual per colony was measured (see sample size in Fig. 1). The genetic data obtained using eight microsatellite markers by Clémencet et al. (2005) were used to compare the genetic and morphological differentiation.

In the laboratory, workers were removed from alcohol, dissected, dried at room temperature and digitally photographed using a Leica XC-ST70 video camera module. Five morphological traits were measured using Matrox Inspector software (to the nearest 0.015 mm): body length from the beginning of the clypeus in top view to the end of the abdomen (BL); tibia length of the right hind leg (TL); scape length, i.e. straight-line distance from base to apex of the scape (SL); head length from the beginning of the clypeus in top view to the end of the head capsule (HL) and head width at the interocular line (HW).

The effect of habitat type (seaside vs. vineyard) on the mean size was tested using an analysis of variance with populations nested within habitat type for each morphological trait. The analysis was performed using the MIXED procedure for nested analysis of variance in SAS 7 for Windows (SAS Institute, Cary, NC) with habitat type defined as a fixed factor and population as a random factor. Morphological divergences between populations were estimated by Mahalanobis D^2 distances using Proc Candisc in SAS (SAS Institute 1996). Compared to Euclidean or Pythagorean distances, Mahalanobis distances have the advantage of incorporating the effects of correlation between morphological variables (Campbell and Atchley 1981). Degrees of genetic divergence among populations were estimated by F_{ST} pairwise coefficients. Levels of association between the matrices of morphological distances (D^2), genetic distances (F_{ST}) and geographical distances (Km) were examined by Mantel's tests (1967). Significance levels were obtained by comparing the distribution of observed values to 10,000 values obtained by random permutation of row and column elements in the independent matrices using XLSTAT-PRO 7.5.

Variation in worker size among colonies

In May 2004, a new sampling was performed to investigate the relationship between nest depth, colony size and worker size. We collected colonies from two populations, one in each type of habitat. Thirteen colonies were sampled in inland population L4 while eleven other colonies were sampled in the seaside population A2. These two populations were included in the previous study and were shown to differ in worker size for the five morphological traits considered (post-hoc test, all $P < 10^{-3}$). Nest excavation was easy because of its predictable structure (see Introduction), but extra care was taken not to miss any room or gallery that might contain ants. The depth of the nest was recorded when we attained the deepest chamber, where the queen was found. In the laboratory, the number of workers in each colony was counted and a sample of 30 randomly chosen workers per colony was measured as described above ($n = 720$). Given that the five previous morphological measures were all highly correlated, only the one with the lowest measurement error (1.3%) was taken, i.e. the tibia length. Measurement error (ME) was assessed by repeated measurements and was quantified as % ME following Bailey and Byrnes (1990) for a set of 10 *C. cursor* individuals encompassing the entire size range.

We first examined if workers from the two populations differed in size using an analysis of variance model, with colonies nested within populations. The analysis was performed using the procedure MIXED of SAS, with population as a fixed factor and colonies within population as a random factor. We examined whether the depth of nest and colony size differed between the two populations and explored the relationship between colony size and depth of nest by standardized major axis (SMA) methods (a type II regression approach; Sokal and Rolf 1995). SMA slope-fitting technique is appropriate when the purpose is to estimate and compare the line of best fit relating two variables each having a random variation. SMAs were fitted for each population individually. Then tests for homogeneity of slopes between populations and calculation of a common slope were conducted following Warton and Weber (2002). When a common slope could be fitted (test of homogeneity, $P > 0.05$), ANCOVA-like comparisons were conducted to test for difference in elevation (intercept) of slopes (i.e. significant difference on the *y*-axis between populations) and separation of the populations along the common slope (i.e. significant difference on the *x*-axis between populations) using SMATR v.1 software (Falster et al. 2003). The same SMA procedure was conducted to examine relationships between means as well as variance in worker size and colony size in both populations.

Results

Variation in worker size among populations

We confirmed that in *C. cursor*, worker size is normally distributed with unimodal distribution and that the five
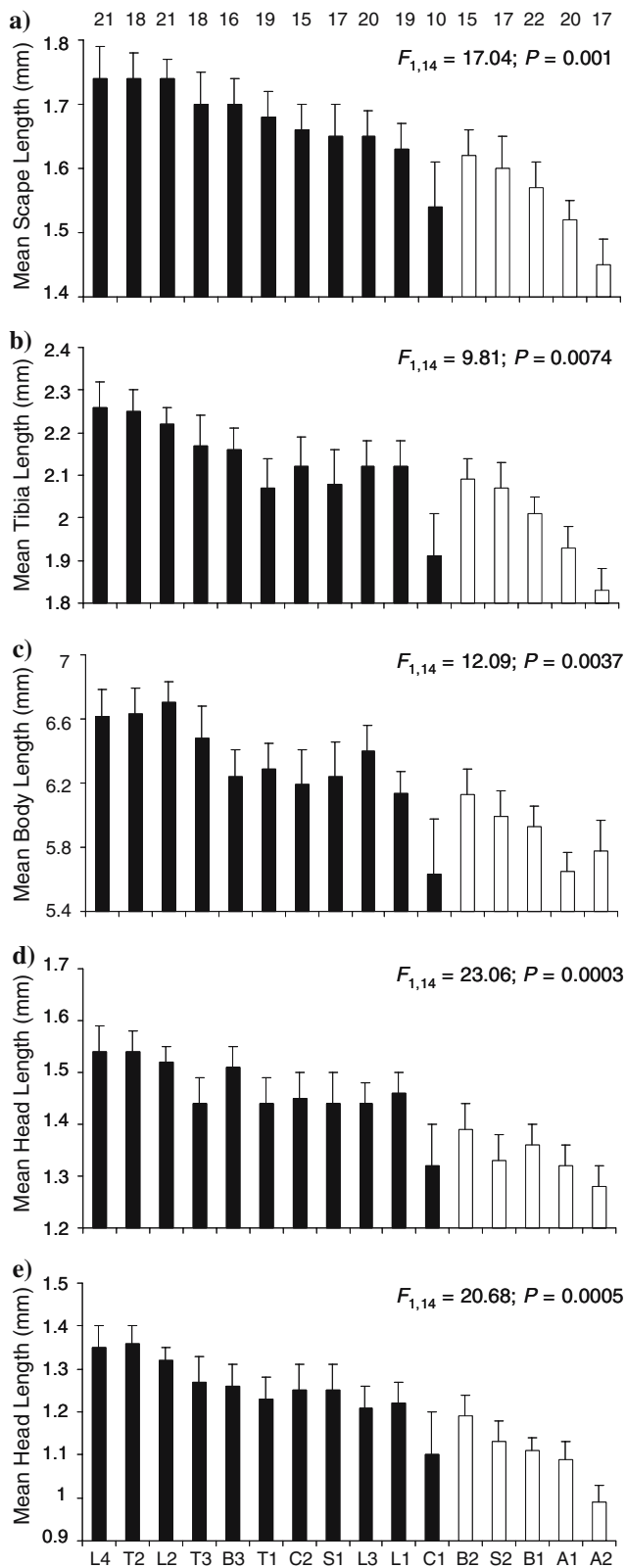
◀ **Fig. 1a–e** Worker-size variation among populations. Morphological measurements [mean ± SE (mm)]: scape (**a**), tibia (**b**), body (**c**) and head length (**d**) as well as head width (**e**) are given for each of the 16 populations studied. The number of workers measured in each population is given above each *bar* in **a**. Seaside populations are represented with *white bars* and vineyard populations with *black bars*. The results of the analysis of variance to test for differences in worker size between habitat types (populations nested within habitat type) are given for each morphological trait. The percentage of the random variance explained by population ranged from 1 to 7.6% and was never significant

variation, ranging from 10.7% for the scape length to 16% for the head width, were very close to those reported by Cagniant (1983). Means (±SE) of the five morphological traits for the 16 populations are given in Fig. 1. The analysis of variance for each of the five morphological traits measured showed that workers from seaside populations were significantly smaller (15% for BL to 19% for HW) than workers from vineyard populations (($P < 0.01$ for the five measurements, Fig. 1). All the vineyard populations except one (C1; $n = 10$) had a mean worker size larger than the seaside populations (Fig. 1). Within a given habitat, workers did not significantly vary in size among populations. The genetic distances (F_{ST}) among populations ranged from 0.006 (T1–T2) to 0.309 (S1–T3), while the Mahalanobis D^2 ranged from 0.065 (T2–L4) to 4.96 (T2–A2). The matrix of morphological distances was neither significantly correlated with the genetic distance ($r = 0.002$; $P = 0.27$) nor with the geographical distances matrices ($r = 0.05$; $P = 0.11$).

Variation in worker size among colonies

As predicted from the habitat type, the mean depth of nests was significantly different between the two populations (Mann–Whitney test, $Z = 3.048$, $P = 0.002$), with nests being on average almost twice as deep in the vineyard (mean ± SE; $m_{L4} = 62.4 ± 22$ cm) than in the seaside population ($m_{A2} = 38.3 ± 9.3$ cm). As expected from the difference in nest structure, mean colony size was almost twice as high in the vineyard population (mean ± SE; $m_{L4} = 1,107.8 ± 485.8$; range$_{L4} = 260$–1,714) than in the seaside population ($m_{A2} = 577.7 ± 275.85$; range$_{A2} = 208$–968; Mann–Whitney test, $Z = 2.636$, $P = 0.008$). Finally, as detected in the previous part of this study by sampling one worker per colony, mean worker size was significantly higher in colonies from the vineyard than from the seaside population ($F_{1,22} = 14.18$; $P = 0.0011$). Colonies explained a nonnegligible part of the random variance component (16%, $P = 0.0024$), indicating that, within a population, mean worker size varied among colonies.

measures taken were highly correlated (correlation coefficients ranging from 0.76–0.92, all significant at $P < 10^{-4}$). Overall size amplitude and coefficient of

In both populations, the depth of nest significantly increased with colony size (see Fig. 2a; $P_{L4} = 0.009$; $P_{A2} = 0.049$), and slopes did not differ between populations ($P = 0.404$). In agreement with the difference in colony size between the two populations, a significant separation along the common slope, i.e. along the x-axis (colony size), was detected between the two populations ($F_{1,23} = 13.03$, $P = 0.002$). No significant difference in the intercept value was detected ($F_{1,23} = 0.274$, $P = 0.6$), indicating that for a given depth of nest, colony size should be the same in both populations. The regression of mean worker size on colony size was significantly positive in both populations studied (see Fig. 2b; $P_{L4} = 0.0066$; $P_{A2} = 0.017$) with the two slopes not significantly different between populations ($P = 0.081$). A significant separation along the common slope, i.e. along the x-axis (colony size), was also detected between the two populations ($F_{1,23} = 14.39$, $P = 0.001$) reflecting the difference in colony size detected between the two populations. Interestingly, no significant difference in the intercept value was detected between the two populations ($F_{1,23} = 0.23$, $P = 0.63$), signifying that, for a given colony size, mean worker size should be the same in both populations. In contrast, the variance in worker size was not related to colony size in either population (see Fig. 2c, $P_{L4} = 0.94$; $P_{A2} = 0.19$). In addition, slopes were not significantly different between the two populations ($P = 0.073$). As observed above, a significant separation along the common slope was detected between the two populations ($F_{1,23} = 9.357$, $P = 0.006$), while no significant difference in the intercept value was detected ($F_{1,23} = 2.367$, $P = 0.138$), indicating that, on average, variance values were the same in both populations.

Fig. 2 Regression of depth of the nest (**a**), mean worker size (**b**) and variance of worker size (**c**) on colony size. *White circles* are colonies sampled in the population A2 at the seaside and *black circles* are colonies sampled in the population L4 in the vineyard. Significance (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) and r^2 values are given for each regression. Equations for the common regression lines are **a** $y = 0.04x + 16.7$, **b** $y = 2.37.10^{-4}x + 1.9$ and **c** $y = -3.88.10^{-5}x + 0.07$

Discussion

C. cursor colonizes two main types of habitats, seaside and vineyard, that differ by an ecological factor, the depth of the water table, which is known to clearly constrain the depth of nest in this species (Cagniant 1976). The water table in the vineyard populations was shown to be deeper than in the seaside populations (Cagniant 1976; H. Cagniant, our observation). We found that the mean worker size was up to 27% smaller (for head width) in the seaside populations than in the vineyard. This result was predicted assuming a positive relationship between worker size and colony size as well as between colony size and the depth of nests. These two positive relationships were verified in both a vineyard and a seaside population of *C. cursor*.
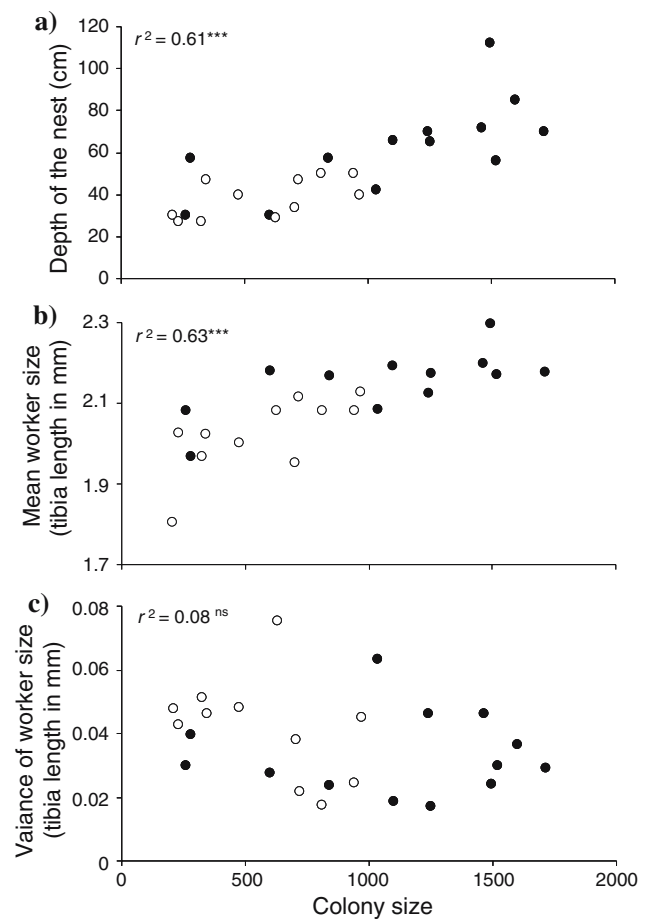
Moreover, the standardized major axis (SMA) method (type II regression) showed that the regression parameters (slope and intercept) were the same in both populations and that the two populations were significantly separated along this common regression line. This indicated that the difference in the depth of nests between the two populations was sufficient to explain the difference in colony size, and that the difference in colony size was sufficient to explain the difference in mean worker size. The largest nests were twice as deep in the vineyard population than at the seaside, with the depth corresponding approximately to the appearance of humid soils (Cagniant 1976; H. Cagniant, personal observation). Interestingly, the maximum colony size was about twice as big in the vineyard as in the seaside population, even though the minimum colony size was

the same (see Fig. 2). It is therefore tempting to conclude that differences in a simple proximate ecological factor can lead to a drastic variation in colony size and mean worker size between populations, two major parameters tightly linked to colony productivity.

It could be argued that other differences, of genetic and/or environmental origins, could also shape the pattern observed between populations. First, given that seaside populations were sampled in a smaller geographical area, genetic similarity or geographical proximity of seaside populations might lead to morphological similarity. However, no significant correlation between morphological and genetic or geographical distances was detected. Second, differences in mating/breeding system may be linked to worker size variation (Oster and Wilson 1978; Frumhoff and Ward 1992; Fjerdingstad and Crozier 2006). For instance, the number of queens per colony has been shown to affect body size of workers in *Leptothorax acervorum* (Heinze et al. 1995), *Solenopsis invicta* (Goodisman and Ross 1996) and *Formica selysi* (Schwander et al. 2005). However, the two *C. cursor* populations that we studied exhibited the same colony organization with a single queen per colony and a high level of polyandry [on average 11.1 ± 3.6 males in the vineyard population and 10.8 ± 2 in the seaside (J. Clémencet et al., personal communication)]. Finally, we cannot rule out that other ecological factors could also differ between the populations studied even though the constraint due to the water table appears to be the most likely. Experimental manipulations are however needed to conclude decisively on the causal link of the relationships observed here. Within the two populations studied, nest depths explained a remarkably high part (62%) of the variation in colony size, a parameter generally supposed to be affected by various ecological and social factors (Bourke 1999). Within populations, variation in nest depths should reflect variation in colony growth and age even though it can still be constrained by micro environmental variations. As suggested by the intercept of the regression line of nest depth and colony size, freshly established propagules settle in shallow nests, which is in agreement with field observations (never deeper that 25–30 cm; personal observation May 2006; Lenoir et al. 1988).

As generally observed in ants (see Brian 1957; Elmes 1974; Wood and Tschinkel 1981; Porter and Tschinkel 1985; Gibson 1989; Tschinkel 1988, 1993, 1998; Wetterer 1994; Kaspari and Byrne 1995), worker size was found to be positively associated with colony size. This pattern is often observed in species with independent colony founding in which queens sacrifice worker size for worker number, the first workers being

the smallest, the so-called nanitic workers (Wilson 1971). This pattern is also commonly observed in ants with clearly polymorphic worker castes. In such cases, the largest worker caste is only produced once the colony reaches a sufficient size, and the increase in mean worker size with colony size is associated with an increase in the variance in worker size (Brian 1957; Gibson 1989). In *C. cursor*, none of these explanations hold since this ant founds colonies dependently and has no distinct worker caste (Cagniant 1983).

The minimum colony size observed in our populations, as well as in populations studied by Lenoir et al. (1988), was around 200. This gives an idea of the minimum propagule size during a colony fission event, and agrees with the observations of Lenoir et al. (1988) estimating around 250 workers as the size of a propagule. Basically, a colony of 200 workers cannot be as energetically constrained as a queen founding a colony alone. Two hypotheses could explain our correlation between colony size and worker size. First, a small colony might not be able to afford the production of large workers because these workers could specialize in particular tasks. Such physical specialization could be costly for a small colony by decreasing its flexibility in response to environmental variation (Wheeler 1991). This explanation based on the division of labor would imply that large workers are produced to increase the variance in worker size and thus increase the efficiency of colonies. The absence of correlation between variance in worker size and colony size goes against this hypothesis. As worker size is normally distributed, it is unlikely that smaller colonies simply do not produce the largest workers. A more likely proximate explanation would be that the level of resources a colony can obtain linearly increases with its size in the colony size range observed in our study. Larger colonies could then obtain more resources leading to a shift of the distribution of worker size toward large size. This would mean that colonies never reached the point at which the curve of the resources gained as a function of colony size becomes asymptotic. Note that species that have a possibility to undergo fission when this critical point is attained should be favored to do so (Tsuji 1995).

From an evolutionary perspective, given that there is a trade-off between the number and size of workers, the increase in worker size with colony size suggests that investing in larger workers rather than in a higher number of small workers is advantageous for large colonies. In thermophilic ants, worker size is generally a major parameter affecting their thermal tolerance (Cerdá and Retana 1997). A higher resistance to temperature in larger workers has also been found in

C. cursor (Clémencet et al., personal communication). In this non-territorial ant, being the most dominated species of the Mediterranean ant community (Cerdà et al. 1997), larger worker size could therefore allow colonies to expand their daily activity period and avoid interspecific competition by foraging mainly during the hottest hours of the day.

In agreement with models that predict an advantage to producing many small workers when colonies are territorial and engage in battles with other colonies (Francks and Partridge 1993; Mc Glynn 2000), in *C. cursor*, the production of many small workers is unlikely to be advantageous in the context of inter- and intraspecific competition. At the colony level, selection should then favor an increase in worker body size since it would enhance the colony's survival or reproduction (Crozier and Consul 1976). However, at the individual level, if the reproductive potential of workers is linked to their size, as has been observed in different species (Tsuji 1995; Heinze et al. 1999; Heinze and Oberstadt 1999; Dietemann et al. 2002; Gobin and Ito 2003; Ravary and Jaisson 2004), individual-level selection should favor the evolution of an optimum size for worker reproduction (Oster and Wilson 1978; Fjerdingstad and Crozier 2006). This optimum might diverge from the one favored at the colony level.

Such conflicting selective pressures potentially occur in *C. cursor*. In this species, unmated workers have been shown to produce both males and females (gynes and workers) by arrenothokous and thelytokous parthenogenesis, respectively, in the absence of the queen (Cagniant 1983). Moreover, workers of intermediate size (between 6.3 and 7.4 mm) appear to produce more eggs than small or large workers (Cagniant 1983). The optimum size for the worker might therefore be different than the one for the colony. The evolution of worker size in this species probably results from many, and probably conflicting, selective pressures and is far from being elucidated.

References

Backus VL (1993) Packaging of offspring by nests of the ant *Leptothorax longispinosus*: parent–offspring conflict and queen–worker conflict. Oecologia 95:283–289

Bailey RC, Byrnes J (1990) A new method for assessing measurement error in both univariate and multivariate morphometric studies. Syst Zool 39:124–130

Blanckenhorn WU, Demont M (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? Integr Comp Biol 44:413–424

Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Bourke AFG (1999) Colony size, social complexity and reproductive conflict in social insects. J Evol Biol 12:245–257

Braendle C, Hockley N, Brevig T, Shingleton AW, Keller L (2003) Size-correlated division of labour and spatial distribution of workers in the driver ant, *Dorylus molestus*. Naturwissenschaften 90:277–281

Brian MV (1957) The growth and development of colonies of the ant *Myrmica*. Insectes Soc 4:177–190

Cagniant H (1976) Distribution, écologie et nid de la fourmi *Cataglyphis cursor* Foscolombe Hyménoptères Formicidae. Vie Milieu 26:265–276

Cagniant H (1983) La parthénogénèse thélytoque et arrhénotoque des ouvrières de la fourmi *Cataglyphis cursor fonscolombe* (Hyménoptères Formicidae) étude biométrique des ouvrières et de leurs potentialités reproductrices. Insectes Soc 30:241–254

Calabi P, Porter SD (1989) Worker longevity in the fire ant *Solenopsis invicta*; ergonomic considerations of correlation between temperature, size and metabolic rates. J Insect Physiol 35:643–649

Campbell NA, Atchley WR (1981) The geometry of canonical variable analysis. Syst Zool 30:268–280

Cerdá X, Retana J (1997) Links between worker polymorphism and thermal biology in a thermophilic ant species. Oikos 78:467–474

Clémencet J, Viginier B, Doums C (2005) Hierarchical analysis of population genetic structure in the monogynous ant *Cataglyphis cursor* using microsatellite and mitochondrial DNA markers. Mol Ecol 14:3735–3744

Crozier R, Consul PC (1976) Conditions for genetic polymorphism in social Hymenoptera under selection at the colony level. Theor Popul Biol 10:1–9

Davidson DW, Cook SC, Snelling RR (2004) Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. Oecologia 139:255–266

Dietemann V, Hölldobler B, Peeters C (2002) Caste specialisation and differentiation in reproductive potential in the phylogenetically primitive ant *Myrmecia gulosa*. Insectes Soc 49:289–298

Elmes GW (1974) The effect of colony population on caste size in three species of *Myrmica* (Hymenoptera: Formicidae). Insectes Soc 2:213–230

Falster DS, Warton DI, Wright IJ (2003) SMATR: standardised major axis tests and routines. Version 1.0. http://www.bio.mq.edu.au/ecology/SMATR/

Fjerdingstad EJ, Crozier R (2006) The evolution of worker caste diversity in social insects. Am Nat 167:390–400

Franks NR, Partridge LW (1993) Lanchester battles and the evolution of combat in ants. Anim Behav 54:197–199

Frumhoff PC, Ward PS (1992) Individual-level selection, colony-level selection and the association between polygyny and worker monomorphism in ants. Am Nat 139:559–590

Gibson RL (1989) Soldier production in *Camponotus novaeboracensis* during colony growth. Insectes Soc 36:28–41

Gobin B, Ito F (2003) Suma wrestling in ants: major workers fight over male production in *Acanthomyrmex ferox*. Naturwissenschaften 90:318–321

Goodisman MAD, Ross KG (1996) Relationship of queen number and worker size in polygyne colonies of the fire ant *Solenopsis invicta*. Insectes Soc 43:303–307

Hansell M (1987) Nest building as a facilitating and limiting factor in the evolution of eusociality in the Hymenoptera. In: Harvey PH, Partridge L (eds) Oxford surveys in evolutionary biology, vol. 4. Oxford University Press, Oxford, pp 155–181

Heinze J, Lipski N, Schlehmeyer K, Hölldobler B (1995) Colony structure and reproduction in the ant, *Leptothorax acervorum*. Behav Ecol 6:359–367

Heinze J, Foitzik S, Oberstadt B, Ruppell O, Hölldobler B (1999) A female caste specialized for the production of unfertilized eggs in the ant *Crematogaster smithi*. Naturwissenschaften 86:93–95

Heinze J, Oberstadt B (1999) Worker age, size and social status in queenless colonies of the ant *Leptothorax gredleri*. Anim Behav 58:751–759

Heinze J, Foitzik S, Fischer B, Wanke T, Kipyatkov VE (2003) The significance of latitudinal variation in body size in a holarctic ant, *Leptothorax acervorum*. Ecography 26:349–355

Hölldobler B, Wilson EO (1990) The ants. Springer, Berlin

Kaspari M, Byrne MM (1995) Caste allocation in litter Pheidole: lessons from plant defense theory. Behav Ecol Sociobiol 37:255–263

Kaspari M (2005) Global energy gradients and the regulation of body size: worker mass and worker number in ant colonies. Proc Natl Acad Sci USA 102:5079–5083

Lenoir A, Querard L, Pondicq N, Berton F (1988) Reproduction and dispersal in the ant *Cataglyphis cursor* (Hymenoptera, Formicidae). Psyche 95:21–44

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220

Mc Glynn TP (2000) Do Lanchester's laws of combat describe competition among ants? Behav Ecol 11:686–690

Ness JH, Bronstein JL, Andersen AN, Holland JN (2004) Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. Ecology 85:1244–1250

Nijhout HF (2003) The control of body size in insects. Dev Biol 261:1–9

Nowbahari E, Feneron R, Malherbe MC (1999) Effect of body size on aggression in the ant, *Cataglyphis niger* (Hymenoptera; formicidae). Aggress Behav 25:369–379

Nowbahari E, Feneron R, Malherbe MC (2000) Polymorphism and polyethism in the formicinae ant *Cataglyphis niger* (Hymenoptera). Sociobiology 36:485–496

Nylin S, Gotthard K (1998) Plasticity in life history traits. Annu Rev Entomol 43:63–83

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton

Porter SD, Tschinkel WR (1985) Fire ant polymorphism: factors affecting worker size. Ann Entomol Soc Am 78:381–386

Ravary F, Jaisson P (2004) Absence of individual sterility in thelytokous colonies of the ant *Cerapachys biroi* Forel (Formicidae, Cerapachyinae). Insectes Soc 51:67–73

Reyes-Lopez JL, Fernandez-Haeger J (2001) Some factors determining size-matching in the harvester ant *Messor barbarus*: food type, transfer activity, recruitment rate and size-range. Insectes Soc 48:118–124

Schwander T, Rosset H, Chapuisat M (2005) Division of labour and worker size polymorphism in ant colonies: the impact of social and genetic factors. Behav Ecol Sociobiol 59:215–221

Sokal RR, Rohlf FJ (1995) Biometry. WH Freeman, San Francisco

Sorvari J, Hakkaraien H (2005) Deforestation reduces nest mound size and decreases the production of sexual offspring in the wood ant *Formica aquilonia*. Ann Zool Fenn 42:259–267

Stearns SC (1992) The evolution of life histories. Oxford University Press, New York

Tschinkel WR (1988) Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. Behav Ecol Sociobiol 22:103–115

Tschinkel WR (1993) Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. Ecol Monogr 63:425–457

Tschinkel WR (1998) Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius*. I. Worker characteristics in relation to colony size and season. Insectes Soc 45:385–410

Tsuji (1995) Reproductive conflicts and levels of selection in the ant *Pristomyrmex pungens*: contextual analysis and partitioning of covariance. Am Nat 146:586–607

Warton DI, Weber NC (2002) Common slope tests for bivariate errors-in-variables models. Biom J 44:161–174

Wetterer JK (1994) Ontogenetic changes in forager polymorphism and foraging ecology in the leaf-cutting ant *Atta cephalotes*. Oecologia 98:235–238

Wilson EO (1959) Some ecological characteristics of ants in New Guinea rain forests. Ecology 40:437–447

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge

Wheeler DE (1991) The developmental basis of worker caste polymorphism in ants. Am Nat 138:1218–1238

Wood LA, Tschinkel WR (1981) Quantification and modification of worker size variation in the fire ant *Solenopsis invicta*. Insectes Soc 28:117–128