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Foreword by the Guest Editor	i
<i>Cataglyphis</i> desert ants: a good model for evolutionary biology in Darwin's anniversary year—A review A. Lenoir, S. Aron, X. Cerdá, and A. Hefetz	1
A checklist of the ants of Israel (Hymenoptera: Formicidae) M. Vonshak and A. Ionescu-Hirsch	33
An annotated list of <i>Camponotus</i> of Israel (Hymenoptera: Formicidae), with a key and descriptions of new species A. Ionescu-Hirsch	57
<i>Monomorium kugleri</i> n. sp.—a new fossil ant species (Hymenoptera: Formicidae: Myrmicinae) from the late Eocene Rovno Amber (Ukraine) A.G. Radchenko and E.E. Perkovsky	99
Sharing versus monopolizing: distribution of aphid sources among nests within a <i>Formica exsecta</i> Nylander (Hymenoptera: Formicidae) supercolony K. Erős, B. Markó, C. Gál, Z. Czekeš, and E. Csata	105
The impact of macro- vs. micro-environmental factors on the structure of ant communities inhabiting East-Mediterranean Aleppo pine forests I. Izhaki, B. Idelovich, R. Laster, and Y. Ofer	129
Seed augmentation has a limited effect on species diversity of sand-dwelling ants U. Segev and Y. Ziv	147
Ant mimicry by <i>Passiflora</i> flowers? S. Lev-Yadun	159
Note: A <i>Camponotus fellah</i> queen sets a record for Israeli ant longevity M. Vonshak and A. Shlagman	165
List of new taxa described in this volume	169
Notes for authors	171

Cover: A queen *Camponotus fellah* Dalla Torre ant surrounded by her workers—offspring tending her in an artificial arena specifically designed by Alex Shlagman. This queen, which lived in this arena for approximately 26 years, died recently, and she is the subject of an article by Vonshak and Shlagman published in this issue (p. 165). Photo: Gil Wizen.

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## ***Cataglyphis* desert ants: a good model for evolutionary biology in Darwin's anniversary year — A review**

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### **ABSTRACT**

*Cataglyphis* ants comprise one of the most characteristic groups of insects in arid regions around the Mediterranean basin and have been intensively studied over the last 30 years. These ants are central-place foragers and scavengers, single-prey loaders that have become a model for insect navigation using sophisticated visual orientation, having lost pheromone orientation. They are highly heat-tolerant ants that forage close to their critical thermal limit during the hottest hours of the day, with their long-chain cuticular hydrocarbons protecting them from desiccation. This is exemplified in two *Cataglyphis* species, each of which developed different mechanisms for counteracting extreme heat when foraging: polymorphism of workers vs. physiological and behavioral adaptations. Several species in this genus have also become a model for studying nestmate recognition mechanisms. The role of cuticular hydrocarbons and the postpharyngeal gland as a reservoir of hydrocarbons in nestmate recognition was initially discovered mainly in *Cataglyphis*, including the first experimental demonstration of the Gestalt model of nestmate recognition. These ants possess very acute discrimination capacities, down to individual recognition. Such fine discrimination is seemingly used by ants that rescue from ant-lion traps only those individuals that are their nestmates. Two main reproductive strategies are exhibited by species of this genus: some reproduce classically, by independent colony foundation following nuptial flight, whereas others reproduce by colony fission. Limited dispersion increases competition for access to resources, and local resource competition

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This article is dedicated to Professor Jehoshua Kugler (1916–2007), a pioneer of ant studies in Israel, who described a new species of *Cataglyphis* from this region (Kugler, 1981).

has been demonstrated. Multiple mating, which had been considered to be rare in ants, has also been reported in all species studied. Finally, the most important discovery in recent years with regard to reproduction strategies in *Cataglyphis* is probably the occurrence of thelytokous parthenogenesis in both workers and queens. In *Cataglyphis cursor*, queens are able to produce new queens by thelytoky, a phenomenon that was later found in four other ant species. This ability does not exist in any other *Cataglyphis* species, attesting to the great variety of reproductive strategies in this genus.

**KEYWORDS:** *Cataglyphis*, orientation, reproduction strategies, thelytoky, parthenogenesis, multiple mating, nestmate recognition, hydrocarbons, xenophily

## INTRODUCTION

*Cataglyphis* ants are one of the most characteristic and conspicuous insects of arid regions around the Mediterranean basin and can be seen running very rapidly, up to 20 meters per minute, during the hottest hours of the day. They are called “the thief of the cooking pot” in Arabic, and “thief” in Greek (due to their rapid stealing of food particles) or “Englishmen” (due to their activity in the hot midday sun at siesta time) (Harkness and Wehner, 1977). A century ago, Santschi (1911) observed the sun-assisted orientation skills of *Cataglyphis* ants in Tunisia (reviewed by Wehner, 1990). During a total eclipse of the sun in June, 1973, in the Sahara Desert, these ants were observed to have remained motionless (Délye, 1974). The genus comprises more than 100 species that are easily identifiable, do not sting, and form small colonies (from hundreds to a few thousand members). They were studied extensively from many aspects, including orientation, systematics, ecology, and reproductive strategies (147 hits with *Cataglyphis* in the title in the Web of Science on February 9, 2010). Despite the wealth of knowledge and the long-term studies by Wehner, mainly in Tunisia on *C. bicolor*, the only semi-popular review article on *Cataglyphis* ants is 30 years old (Harkness and Wehner, 1977). The present review, in honor of the late Prof. J. Kugler, was written in a Darwin anniversary year (200th anniversary of his birth and 150th of his book *On the Origin of Species*). As in many articles pertaining to evolutionary theory that were written in homage to Darwin (see, for example, Evolution. *Nature* 457(7231): 807–848), we delved into the evolutionary biology of *Cataglyphis*. We aimed at showing why the genus *Cataglyphis* constitutes a good model for addressing numerous questions studied by evolutionary biologists from a Darwinian perspective, while integrating both published and unpublished data.

## EVOLUTIONARY BIOLOGY OF *CATAGLYPHIS*

### 1. Ecology

Ecologically, the ant genus *Cataglyphis* is fairly homogeneous: it is widespread over the arid regions of the Old World, characterized by a strictly diurnal activity, and is highly

thermophilic (Wehner et al., 1983; Cerdá et al., 1989; Lenoir et al., 1990; Cerdá and Retana, 1997). The genus comprises species that inhabit arid lands and deserts, including the Sahara, Near East and Middle East, Arabian Peninsula, and Central Asia. Apparently, *C. fortis* is the only species to inhabit salt-pan areas such as chotts in North Africa's deserts, a highly inhospitable habitat (Dillier and Wehner, 2004). Nest demography and architecture have been described for only a few species and reveal strong ecological constraints on colony size. For example, in *C. cursor*, nest depth is positively correlated with colony size (Clémencet and Doums, 2007) so that near the Mediterranean Sea the adjacent high water table level restricts the depth and size of colonies compared to more inland areas.

Most of these arid areas are resource poor, necessitating long foraging distances and, accordingly, the ants evolved superior navigational abilities (Wehner et al., 1983; Wehner et al., 1994). From an ecological point of view, they are central-place foragers, single-prey loaders, and are scavengers rather than harvesters or predators. They are part of the pollinator assemblage of certain insect-pollinated flowers (Herrera et al., 1984; Ortigosa and Gómez, in press) and contribute to seed-dispersal of some myrmecochorous and non-myrmecochorous plants (Hulme, 1997; Boulay et al., 2007). With the sole exception of *Cataglyphis floricola*, which uses petals as its main food source (Cerdá et al., 1992, 1996), all *Cataglyphis* species feed mainly on dead arthropods (Délye, 1968; Wehner et al., 1983; Cerdá, 1988; Cerdá et al., 1989; Cerdá and Retana, 1997). As these constitute an unpredictable food source, the ants forage individually and do not use any modes of recruitment other than performing simple invitation behavior when a food source is discovered (Szlep, 1973; Amor et al., 2010), as observed in other ant species that display individual foraging. They have seemingly lost the ability for pheromone orientation and use only chemical signposts at the entrance of the nest (see Nest Defense and Territory section).

#### *Worker activities outside the nest: foraging and social carrying*

*Cataglyphis* workers follow classical age-dependent polyethism, although this was described in different terms by different authors. *Cataglyphis bicolor* workers initially remain inside the nest for about 28 days—first as callows, then as repletes and interior workers—before becoming foragers (Schmid-Hempel and Schmid-Hempel, 1984). *Cataglyphis cursor* workers are initially inactive, then perform various tasks inside the nest (non-specialized activities, nurses, and pre-foragers) before becoming foragers. However, only one-third of the individuals follow this classical age-dependent development, whereas the remainder show either fixed behavior or irregular deviations from the expected scheme (Retana and Cerdá, 1990, 1991). Foraging activity of colonies is diurnal, with the greatest activity taking place during the midday hours when soil temperatures are highest (see, for example, *C. iberica* daily foraging activity in Fig. 1), a pattern that is very consistent in the genus (Harkness, 1977b; Baroni Urbani and Aktaş, 1981; Wehner et al., 1983; Cerdá et al., 1989; Lenoir et al., 1990; Petrov, 1991; Cerdá and Retana, 1998; Cerdá and Retana, 2000). Seasonal activity is strongly influenced by the ant's life cycle: the presence of larvae increases energetic requirements of colonies,

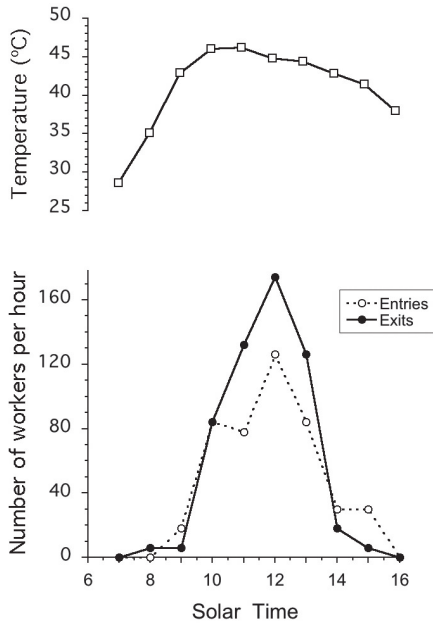


Fig. 1. Daily foraging activity of a *Cataglyphis iberica* nest and ground surface temperature during a summer day (August 1, 1983, Bellaterra, Spain). Entries and exits were measured for 5 min every half hour throughout the activity period; observed values were extrapolated to values per hour.

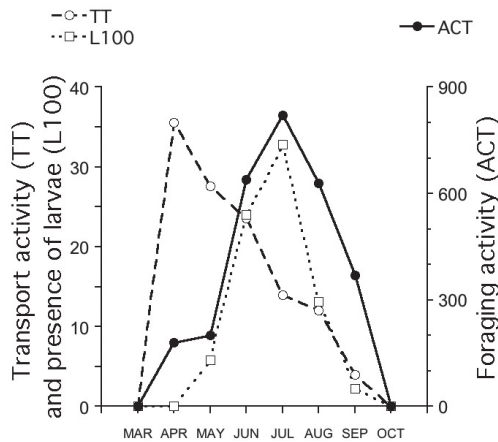


Fig. 2. Seasonal variation of *Cataglyphis iberica* adult transport activity (TT), foraging activity (ACT) and brood presence (L100). Foraging activity is coupled with brood presence, but not with adult transport. Adult transport is at a maximum after hibernation in order to regain a uniform colony odor in all the nests. TT per day and nest: sum of workers carrying a nestmate entering or leaving the nest; ACT per day and nest: sum of workers entering and leaving the nest with or without a prey; L100: presence of larvae; to avoid the effect of colony size, we recorded worker and larvae population in each nest and standardized the number of larvae per 100 workers. (Modified from Cerdá et al., 1994).

Table 1

Critical Thermal Maximum (CTM, in °C) and Maximal Activity Temperature of Foraging (MAT, in °C) of some *Cataglyphis* species present in the Iberian Peninsula. CTM is the temperature at which at least 50% of workers died or lost muscular coordination after 10 min of exposure. MAT is the temperature at which the species displays maximum foraging activity in the field. (Data from Cerdá et al., 1998; Cerdá, 2001)

Species	CTM	MAT
<i>C. cursor</i>	50	48
<i>C. floricola</i>	50	44
<i>C. iberica</i>	52	50
<i>C. rosenhaueri</i>	50	44
<i>C. velox</i>	54	46

thus maximum foraging activity always takes place when the abundance of larvae is highest (Fig. 2) (Bosch et al., 1987; Cerdá et al., 1994).

*Cataglyphis* species are highly heat-tolerant ants whose behavior is risk-prone (Cerdá et al., 1998). Since they forage very close to their critical thermal limits, they run a high risk of mortality due to thermal stress (Table 1). However, their heat-tolerance enables the ants to benefit from this foraging behavior. In Sierra de Palomares (Jaen province, southern Spain), the ant community includes two *Cataglyphis* species, *C. velox* and *C. rosenhaueri*, which are the least behaviorally-dominant species (they quickly left or were driven away from baits upon encountering a higher-ranked and more aggressive species). However, despite the significant decline in their numbers at pitfalls and baits when more dominant-species densities increased, the mean number of *Cataglyphis* workers per bait and their foraging efficiency did not differ among plots that varied in the abundance of dominant species (Cerdá et al., 1998). If foraging periods of *Cataglyphis* were restricted by interference from dominant species, they would be expected to forage over a broader range of times, when dominant species were absent, albeit always within their physiological limits. However, the daily activity rhythms of *Cataglyphis* species were similar in all three zones despite the different abundance levels of dominant ant species, indicating no effect of dominant species on *Cataglyphis* foraging times (Cerdá et al., 1998).

Although risk-proneness gives *Cataglyphis* species an ecological advantage with regard to habitat exploitation, the individual workers are subjected to high thermal stress. Field censuses on individually marked *C. bicolor* workers in Tunisia showed a constant daily loss of 16% of individuals (Schmid-Hempel and Schmid-Hempel, 1984). These losses were correlated with the high mortality risk that the foragers incurred, particularly substantial predation pressure, but probably thermal stress, as well. Life expectancy of forager workers is only 6.1 days (Schmid-Hempel and Schmid-Hempel, 1984). Nonetheless, during this short period of adult life, they exhibit a remarkable increase in size of the mushroom bodies in the brain (Kühn-Buhlmann and Wehner, 2006), presumably



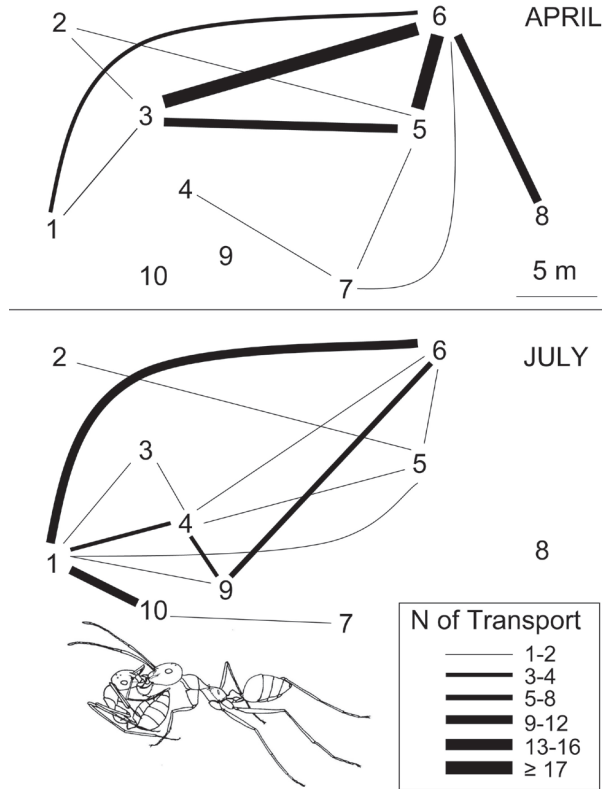


Fig. 3. Network of inter-nest social carrying relationships in a *Cataglyphis iberica* polydomous colony in April and July. Relationships and intensity of transport change between months. The “central” nest contains the only queen of the colony, and centralizes the interchange of workers between nests (central nest was #6 in April and #1 in July). Width of lines indicates the number of adult transports between nests (observations: one hour per nest for four 15-min periods per day). Bottom drawing shows worker position during adult transport (Modified from Cerdá et al., 1994 and Fourcassie et al., 2000); drawing courtesy of A. Lombarte and A. Tinaut.

supporting their high navigation skills. *Cataglyphis* workers may have relatively neotenuous brains, and thus more flexibility, allowing them to adapt neurologically to their environment (Seid and Wehner, 2009). *C. velox* foragers have a more developed immune response (estimated as phenoloxidase and prophenoloxidase activity) compared to inside-nest workers. Such high immune investment is favorably selected since activities out of the nest increase infection risk and the danger of contaminating the entire colony (Bocher et al., 2007). In the central Sahara Desert, the silver ant, *C. bombycina*, is the only arthropod that forages in the full midday sun, even when surface temperatures exceed 60 °C. This species is apparently forced to exploit an extremely narrow thermal

window, the upper and lower limits of which are set by heat stress and predatory pressure, respectively (Wehner et al., 1992).

Social carrying of nestmates, or adult transport (Fig. 3), is a very common and conspicuous phenomenon in *Cataglyphis*, and one which seems to have several purposes, depending on the species. The first description of social carrying was reported for *C. bicolor* by Cornetz (1910). It is assumed that its primary evolutionary function in ants was to serve as a recruitment method during emigrations (see review in Hölldobler and Wilson, 1990), which still holds true for many ant species including, for example, *C. iberica* (Cerdá and Retana, 1998; Dahbi et al., 2008). Similar to several other species of *Cataglyphis*, *C. iberica* is polydomous, with each colony featuring one nest that coordinates the interchange of workers between neighboring satellite nests. This central nest lodges the queen and frequently has the highest number of workers, the highest foraging activity, and the highest rate of worker exchange (Fig. 3) (Cerdá et al., 1994). Polydomy enhances habitat exploitation because foraging activity per colony increases with the number of nests, as do foraging efficiency and prey input (up to a certain colony-size threshold) (Cerdá et al., 2002). Polydomy also serves as an efficient mechanism for nest relocation when a nest is attacked by competitors (Cerdá and Retana, 1998). In polydomous *Cataglyphis* colonies (e.g., *C. bicolor* in Tunisia and *C. iberica* in Spain), social carrying is used for exchanging workers between satellite nests (Cerdá et al., 1994) (Schmid-Hempel and Schmid-Hempel, 1984), providing a mechanism that extends the influence of the queen to all colony members, thus maintaining colony cohesion and presumably also a uniform colony odor (Dahbi et al., 1997). Adult transport is also involved in other colony functions, such as mobilizing soldiers outside the nest, as demonstrated in *C. bombycina* (Délye, 1957), worker repartition after new nests were created by fission, in *C. cursor* (Lenoir et al., 1988), and transportation of workers to the foraging areas, as observed in Greek populations of *C. bicolor* (Harkness, 1977a). In spite of considerable variability (daily, seasonal, annual, spatial), there is a general seasonal pattern in adult transport (e.g., in *C. iberica*), with a peak in transport during early spring, when colonies exit hibernation (Fig. 2) (Cerdá et al., 1994; Dahbi et al., 1997).

### Orientation

In the last few decades, *Cataglyphis* ants have become model organisms for the study of insect navigation. Most of the relevant experiments were performed in Tunisia by Wehner and coworkers. As Wehner has recently published a comprehensive review of this work (Wehner, 2008; and see also Collett and Collett, 2009), we mention here briefly only the main points. Detailed studies that followed Santchi's (1911) first observations on visual orientation in *Cataglyphis* revealed that the ants orient mainly by means of vector navigation (path integration) and landmark-guidance mechanisms, as well as by systematic-search and target-expansion strategies. Vector navigation encompasses information acquisition both with regard to directions steered (compass information) and distances covered (odometer information). Surprisingly, in *C. fortis*, distance estimation and homing performance are unaffected by severe interference with walking behavior (such as leg amputation or uneven substrate) (Steck et al., 2009b), and repeated



training does not improve the path integrator (Merkle and Wehner, 2009). For example, when adult transport in *C. iberica* ants is interrupted, the transporters continue directly to the destination while the transported ant flees in the other direction. This confirms that transporters have a memory of the compass direction of the nest and adjust their course by using a sequence of landmarks. In contrast, transported ants, probably young individuals, seem to use essentially celestial cues (Fourcassie et al., 2000). *Cataglyphis* ants have also become a model for studies in neurobiology of brain development, such as postsynaptic integration in visual navigation (Seid and Wehner, 2008). The ant brain appears to be relatively neotenus and thus more flexible than that of other insects, allowing them to neurologically adapt to the environment. This neoteny observed in *C. albicans* may explain in part the neural basis for age-dependent polyethism and the behavioral flexibility of ants (Seid and Wehner, 2009).

Contrary to the idea that *Cataglyphis* uses only visual orientation, it has been recently demonstrated that *C. fortis* potentially also uses olfactory landmarks to locate their nests (Steck et al., 2009a), which are usually located in salt-pan habitats. Despite its homogenous appearance, the flat ground in these habitats varies slightly in soil structure, and its surface is occasionally interrupted by fissures or pieces of wood and halophytic plants, signs of past periods of flooding. The soil around the nest entrance was shown to contain four aldehydes (hexanal, octanal, nonanal, and decanal) as well as camphor, all common plant volatiles that serve as an olfactory beacon at the nest entrance. The question of whether ant-originated hydrocarbons are also used as landmarks remains open. These are deposited on the ground around the nest and used for nest defense (see below). In *Lasius niger*, the quantity of hydrocarbons (HCs) decreases from the nest entrance towards the foraging arena (Lenoir et al., 2009). The possibility cannot be excluded that a similar process occurs in some *Cataglyphis* species, with HC concentration decreasing with the distance from the nest and being used for orientation to the nest.

#### *Adaptation to arid climates*

In the Sahara Desert, *Cataglyphis* species are extremely thermo-tolerant, in particular with respect to their small size. They forage at body temperatures of above 50 °C, and their critical thermal maxima are at  $53.6 \pm 0.8$  °C for *C. bombycina* and  $55.1 \pm 1.1$  °C for *C. bicolor* (Gehring and Wehner, 1995). Similar values have been observed in other *Cataglyphis* species from Spain (Table 1). One of the mechanisms allowing this high thermal resistance is the existence of Heat Shock Proteins (HSP) in the genus. In *Cataglyphis*, unlike *Drosophila* for instance, these proteins are synthesized even at low temperatures, resulting in their accumulation in the body. This is interpreted as pre-adaptation since it enables the ants to move instantly from an inner nest temperature of less than 30 °C to an outdoor temperature of above 50 °C without being critically affected (Gehring and Wehner, 1995).

Notwithstanding, HSPs are not the only mechanism employed by *Cataglyphis* to withstand thermal stress. Different species in the genus developed alternative (but not mutually exclusive) morphological, physiological, and/or behavioral mechanisms to enable foraging at extreme temperatures. This is exemplified in the study of two

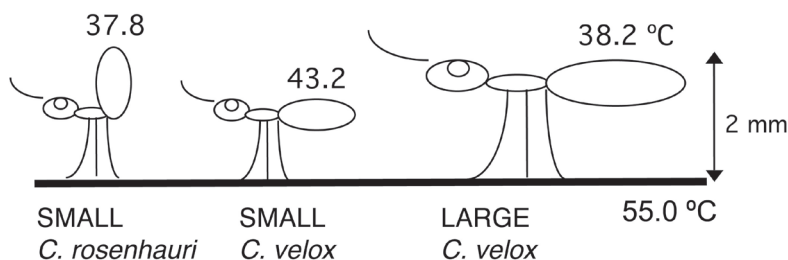


Fig. 4. Schematic view of gaster temperatures (°C) at different heights above the ground in different *Cataglyphis* size workers of *Cataglyphis rosenhaueri* and *C. velox* when soil surface temperature was 55 °C. For *C. rosenhaueri* workers, measures were taken with the gaster in an extended position (comparable measure to that taken in *C. velox*) and in a raised position (the natural position for this species at high soil temperatures) (Modified from Cerdá, 2001).

sympatric *Cataglyphis* species with comparable daily foraging activity patterns from southern Spain: the highly polymorphic *C. velox* (worker length range of 4.5–12 mm), and the less polymorphic *C. rosenhaueri* (worker length range of 4.5–7.5 mm) (Cerdá and Retana, 1997; Cerdá and Retana, 2000). Foraging efforts of *C. velox* were shown to be partitioned among the different worker sizes according to the ambient temperature: very small and small workers foraged preferentially in the morning hours, whereas the major foraging force at midday comprised mainly medium-sized and large workers. On the other hand, *C. rosenhaueri* workers, small and large alike, were active outside the nest throughout the day, especially at midday, when temperatures were at their highest. Thus, despite the comparable Critical Thermal Maximum of both species (CTM of very small, small, medium, and large workers of both species were 50, 52, 54, and 56 °C, respectively), small *C. rosenhaueri* workers withstand high ground temperature better than small *C. velox* workers. Measures of three parameters that pertain to cuticular transpiration, i.e., percentage of transpiratory water loss, cuticular transpiration rate, and metabolic rate (oxygen consumption rate), revealed that small *C. rosenhaueri* workers resemble medium and large *C. velox* workers more than small ones. There are also considerable behavioral differences between the two species. *Cataglyphis velox* workers, irrespective of size, kept their body in a horizontal position, with head and gaster close above the ground surface (Fig. 4). Therefore, large workers that have very long stilt-like legs are able to rise above the hot substrate and to achieve a high running speed, and thus continue to forage, whereas small workers are more vulnerable to heat emanating from the ground at extreme midday temperatures. In contrast, *C. rosenhaueri* workers raised both head and gaster 0.2–0.4 mm higher compared to *C. velox* individuals of similar size (Fig. 4). This behavioral mechanism exhibited by *C. rosenhaueri* foragers provides a good substitute for the long legs of large *C. velox* workers that hold their gaster at a similar (and even greater) height above the ground. Consequently, at ground temperatures of 55 °C, small *C. rosenhaueri* had gaster temperatures that were 6.4–6.6 °C lower

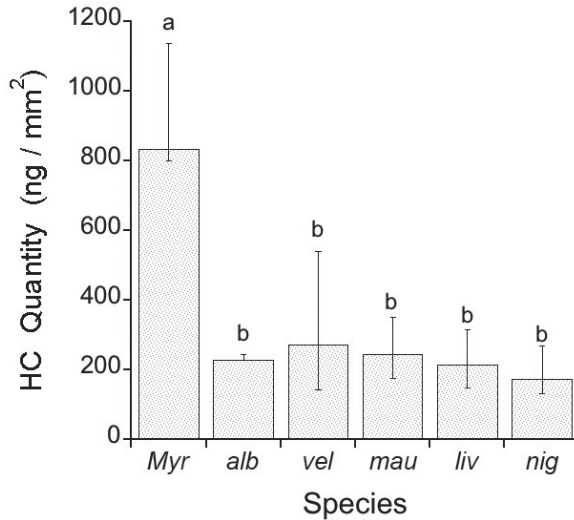


Fig. 5. Hydrocarbon quantities per unit surface (median ng/ mm<sup>2</sup> ± first and third quartiles) for: Myr = *Myrmica rubra*; alb = *Cataglyphis albicans*; vel = *C. velox*; mau = *C. mauritanica*; liv = *C. livida*; nig = *C. niger* (n = 6 to 16 per group). C15 is used as internal standard.

compared to small *C. velox* workers, and similar to the gaster temperatures of large *C. velox* workers. These very different mechanisms probably reflect two independent pathways that evolved in order to withstand extreme thermal conditions. It has recently been confirmed that in *C. cursor* of intermediate size range (3.5–10 mm), large workers are more resistant to high temperatures than small workers (Clémencet et al., 2010).

#### *Cuticular hydrocarbons and adaptation to arid climates*

Water conservation is a challenge for terrestrial organisms, in particular species living in arid habitats. Composition and quantity of cuticular hydrocarbons are considered pivotal in the resistance of insects to desiccation (Hadley, 1981; Lockey, 1985). Many studies have indeed shown a positive correlation between the quantity of cuticular waxes and transpiration in insects and arachnids (Hadley, 1981). Nevertheless, there are also exceptions, as shown in a study of five species of desert beetles, in which no such correlations were found (Hadley, 1978). Cuticular hydrocarbon quantities may be an important factor in preventing desiccation, but data are scarce and sometimes difficult to compare due to differences in calculation methods with internal standards.

We compared several *Cataglyphis* species that forage at high temperatures, when other insects in such arid places remain hidden, to *Myrmica rubra*, an ant that inhabits humid habitats in temperate climates. It was found that all *Cataglyphis* species had 170–270 ng/mm<sup>2</sup> hydrocarbons compared to 800 ng/mm<sup>2</sup> for *M. rubra* (A. Lenoir and D. Marsault, unpublished data; and Fig. 5; but, see Lahav et al., 1998, for a different value for *C. niger*). The present comparison, using the same mode of calculation, clearly

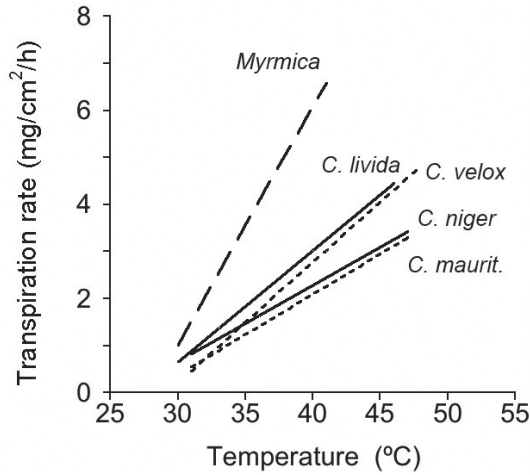


Fig. 6. Worker transpiration rate. *Myrmica rubra* (n = 3), *C. velox* (n = 17), *C. mauritanica* (n = 21), *C. livida* (n = 7) and *C. niger* (n = 10). Ants were placed in desiccators for 75 minutes.

shows that the high hydrocarbon quantity is not essential for protection against desiccation in ants. Despite their lower hydrocarbon amounts, *Cataglyphis* ants lose less water than *Myrmica* ants (Fig. 6). The lethal temperature for *Cataglyphis* was above 50 °C for all species studied (Cerdá et al., 1998; see above) but 39 °C for *Myrmica rubra* (A. Lenoir and D. Marsault, unpublished data). Cuticular water loss per unit surface of workers of different sizes in the polymorphic species *C. velox*, *C. niger*, and *C. mauritanica* is the same in both small and large ants. Small ants, however, are handicapped by their surface-to-volume ratio: they lose 25–35% water at 45 °C whereas large ants lose only 12% water and therefore are more resistant to high temperatures (A. Lenoir and D. Marsault, unpublished data).

Does the quality of the cuticular hydrocarbons matter? Arthropods inhabiting warm, dry environments tend to have longer-chain hydrocarbons than their counterparts in more mesic environments (Hadley, 1981). This is corroborated by the fact that in *M. rubra* inhabiting humid environments, cuticular hydrocarbons include components that are lighter than 3MeC27, whereas *Cataglyphis* species possess large quantities of HCs that are heavier than C27. However, it is impossible to make generalizations based on a single mesic species, as some *Formica* species (such as *F. truncorum*) from northern forests also have long-chain hydrocarbons (Akino, 2006). Unsaturation probably affects cuticle permeability as well: alkenes represent 12% of hydrocarbons in *M. rubra*, while being absent in *Cataglyphis* (A. Lenoir and D. Marsault, unpublished data). In conclusion, based on the limited study of *Myrmica* and the above-mentioned *Cataglyphis* species, adaptation to arid environments in ants does not appear to be related to hydrocarbon

quantities in the cuticle but more likely to their relative composition; i.e., the absence of alkenes and abundance of saturated longer-chain hydrocarbons.

#### *Nest defense and territory*

Most ants defend a territory (Hölldobler and Wilson, 1990). However, this seems to be rarely the case in *Cataglyphis*, which may occasionally defend the nest but seldom possess extended territories. Accordingly, we know of but a few species of this genus that have special guards: in *C. velox*, large workers defend the entrance to the nest (X. Cerdá, unpublished data), whereas in the famous saber-jawed soldiers of *C. bombycina*, “these formidable-looking individuals rush at any moving object when the nest is disturbed” (Hölldobler and Wilson, 1990, p. 330; see also Délye, 1957). However, it appears that this latter species is the only one that has these soldiers, which are not present in the sibling species *C. sabulosa* (Kugler, 1981). In *C. cursor*, field observations indicate that there is no defended territory, including the entrance to the nest, and that there is up to 50% overlap in colony home ranges. Moreover, aggression between workers is rare, even around food sources, which are shared peacefully. As mentioned above, the entrance to the nest is not defended, but, although aliens can enter the nest, they quickly reemerge (Lenoir et al., 1990). These may be deliberate attempts to enter the nest of another colony with the purpose of stealing food or brood. When a colony is excavated in the field, many workers, and particularly callows, are robbed by workers of neighboring colonies (Lenoir et al., 1990). Laboratory experiments showed that the entrance to the nest is marked with fecal spots and that aggression is enhanced if the resident is standing on its own marks. However, aggression is manifested by only 50% of the workers (Mayade et al., 1993). The readiness to fight conspecific ants in *C. cursor* is higher in older than in younger workers and in larger than in smaller workers (Nowbahari and Lenoir, 1989; Nowbahari et al., 1999). Such readiness also occurs near the nest entrance in *C. fortis*, declining at 5 meters (Knaden and Wehner, 2003). Similar territory-dependent aggression was reported in *C. niger*, where workers mark their territory with the cloacal gland secretion and employ the bourgeois strategy when encountering alien conspecific ants (Wenseleers et al., 2002). It would be interesting to investigate the role of this gland in other species. The above findings indicate that, in *Cataglyphis*, when aggressive behavior is present, it is linked to nest defense rather than to food or territory defense. Assuming that cuticular hydrocarbons act to elicit aggression because they are more volatile at higher temperatures (see above), this may result in recognition errors and therefore be too costly. Moreover, *C. fortis* is more aggressive against members of a colony with which they have recently exchanged aggression than against members of a previously unfamiliar colony (Knaden and Wehner, 2003). This suggests a learning recognition process called “enemy-specification” (Wilson, 1975; Carlin and Johnston, 1984), which could be considered as the opposite of the “dear-enemy” phenomenon, in which neighbors that have had multiple encounters are less aggressive in future encounters compared to non-neighbor colonies. Learning abilities and their impact on behavior in ants may be much more developed than considered to date. Using the habituation/discrimination paradigm (decrease of response towards the same stimulus; individual/high

response towards a new stimulus, if it is discriminated), it has been shown that *C. niger* workers are able to recognize previously encountered individuals, whether conspecific or heterospecific (Nowbahari, 2007; Foubert and Nowbahari, 2008).

## 2. Nestmate recognition and the Gestalt

Studies with several *Cataglyphis* species have also laid the groundwork for understanding the basic mechanisms of nestmate recognition, a process by which social animals discriminate between members of their own colony and conspecific aliens. Such discrimination allows the maintenance of colony insularity against competitors and would appear to have played an important role in the evolution of eusociality (Wilson and Hölldobler, 2005). Recognition involves the perception of emitted cues (signals) on the one hand, and pattern comparison with a neural template on the other hand, by the encountering ants. Cuticular hydrocarbons are generally considered as playing an important role in this discrimination (see recent reviews by Hefetz, 2007, and d'Ettorre and Lenoir, 2009). Both aspects of nestmate recognition were studied using several *Cataglyphis* species. The involvement of cuticular hydrocarbons in signal formation was first demonstrated in correlative studies using *C. cursor* and *C. iberica* (Nowbahari et al., 1990; Dahbi et al., 1996). This was followed by a more causative demonstration in *C. niger* (Lahav et al., 1999). In the latter case, it was further shown that the signal is stored in the postpharyngeal gland and permanently exchanged by trophallaxis and grooming between members of the colony, constituting a gestalt (Soroker et al., 1994; Dahbi and Lenoir, 1998a; Dahbi et al., 1999; Lahav et al., 2001). While the existence of a gestalt colony odor was postulated earlier on theoretical grounds, it was first demonstrated in *Cataglyphis* ants and is now an acknowledged basic concept in nestmate recognition. In the polydomous species *C. iberica*, inter-individual transport between nests is a tool for maintaining uniformity of the colonial odor after hibernation (see Adult Transport, above) (Dahbi et al., 1997).

An interesting helping behavior was recently observed in *C. cursor*: workers tied with a nylon thread and partially buried under sand were rescued by congeners. It is noteworthy that only nestmates were rescued, indicating a clear nestmate recognition. Alarm pheromones seem to attract the foragers, but the actual rescue is performed only upon direct or very close contact and may involve Hydrocarbons (Nowbahari et al., 2009; Nowbahari and Hollis, 2010).

Another major question relating to whether colony odor originates from the queen (i.e., the queen produces the signal that is subsequently distributed throughout the colony), or constitutes a true worker-derived gestalt, was also studied in *Cataglyphis*. At least in *C. niger*, the worker-derived cue hypothesis was shown to prevail (Lahav et al., 1998). The queen seems to have a specific cuticular hydrocarbon composition in *C. iberica* (Dahbi and Lenoir, 1998b), as was also found in many other species, and these odor differences appear to be motivational; the queen is attractive to workers and they reduce their activity in her absence (Berton et al., 1992). Larvae also carry colony-specific signals (Lenoir, 1984; Isingrini and Lenoir, 1988).



The chemical integration of callow ants was studied in some *Cataglyphis* species, in which it was shown that callows have very small quantities of hydrocarbons on the cuticle and in the postpharyngeal gland, which increase after a few days of maturity (Soroker et al., 1995; Dahbi et al., 1998). This phenomenon was named “chemical insignificance”, followed by “chemical integration” (Lenoir et al., 1999), and was found to be common in social insects (see, for example, recent papers on wasps, e.g., Cini et al., 2009). Chemical insignificance is a strategy that is sometimes used by parasites (for example, *Acromyrmex insinuator*) and some myrmecophiles to integrate into the host society (Lambardi et al., 2007; Witte et al., 2008). It is also a putative explanation for the tolerance of some guests, such as snakes, in *Atta* nests (Baer et al., 2009).

Chemical integration by mimicry is the means generally used by many parasites and guests to enter ant colonies (Lenoir et al., 2001; Akino, 2008). Only two putative inquiline species are known in the genus *Cataglyphis*: *C. hanna*e, found in *C. bicolor* nests from Tunisia (Agosti, 1994), and *C. zakharovi*, found in a nest of *C. setipes* from Turkmenistan (Radchenko, 1997). The latter inquiline species was described on the basis of only two males and two females. Nothing is known about its biology or chemistry.

Charles Darwin was an enthusiastic beetle collector and used beetles to illustrate different evolutionary phenomena (see Beutel et al., 2009), but he was unaware of myrmecophiles and their coevolution with ants. Myrmecophiles generally mimic the odor of the ant colony. *Thorictus* beetles are known to grasp at one antenna of the host with their mandibles and remain on the same worker for long periods. We found a new species, *Thorictus martinezi*, in nests of *Cataglyphis* sp. from Burkina Faso (Háva and Lenoir, 2008), individuals of which are readily adopted after a day or two in *Cataglyphis* sp. colonies, but when assayed with *C. viatica*, they remain for weeks in the foraging arena without entering the nest. When introduced into a *Formica selysi* colony, the beetles are ignored and rapidly die. These beetles have the same hydrocarbon profile as their host, suggesting a possible coevolution between guest and host (A. Lenoir, unpublished data). This can also explain host species-specificity, as the hydrocarbon profiles of different *Cataglyphis* species are sufficiently different (see Section 3), and as also hypothesized for the caterpillars of *Maculinea* and their *Myrmica* hosts (Elmes et al., 2002).

Template formation (defined as the internal neural model) has also been investigated in *C. cursor*. It appears that the template is largely learned by nestmates through contact with members of the colony, even in immature stages. Larvae are able to learn and memorize the colony odor, and this learning is extended to the first days of adult emergence (Isingrini et al., 1985). While post-imaginal learning of colony odor has been largely confirmed, pre-imaginal learning was studied and confirmed in only one *Camponotus* species (Carlin and Schwartz, 1989). Callow workers learn the odor of their maternal queen but are also able to learn the odor of an alien queen although they do not forget their maternal queen odor, which continues to be attractive to them. This phenomenon can probably be explained by pre-imaginal learning (Berton et al., 1991). All these data show that nestmate recognition in ants is mainly learned early on in life, and thus the ants behave more altruistically in regard to fellowship (or nestmateship) than kinship (Jaisson, 1991; Lenoir et al., 1999).

### 3. Systematics. New tools: hydrocarbons and DNA

Modern taxonomy uses new tools such as mitochondrial DNA and the vast project of DNA bar-coding (Hebert and Gregory, 2005). Although bar-coding is now used in some ant groups such as *Myrmica*, it is limited by the amount of genetic information currently available and cannot yet serve as a universal tool for species demarcation (Jansen et al., 2009). Integrative taxonomy using multiple methodological approaches is necessary to reduce error rates from 30% when using a single type of data to 3% when using three types (always including morphology and genetics) (Schlick-Steiner et al., 2010). Moreover, the number of cryptic species in ants seems to be particularly high, reaching 40 to 50% in some genera according to Seifert (2009), confirming the necessity for a multifactor approach.

Using cuticular hydrocarbons, mtDNA haplotypes and morphology were shown to be efficient in termite taxonomy (Jenkins et al., 2000). In arthropods in general, hydrocarbons are also a good taxonomic tool (Bagnères and Wicker-Thomas, 2010). *Cataglyphis* has been studied extensively from these perspectives, mainly using chemosystematics, but the work is far from being complete as only some groups and geographical regions were investigated. For example, cuticular hydrocarbon-based chemotaxonomy exists for *Cataglyphis* from Spain (Dahbi et al., 1996), Morocco, and Burkina Faso (Dahbi et al., 2008), and for the *C. bicolor* group from Tunisia (Oldham et al., 1999; Gökçen et al., 2002; Wehner et al., 1994). Mitochondrial DNA has been used only for a few species, and although these are not sufficient to construct a complete picture, some partial results can be presented. For example, the previously described species “*C. bicolor*”, from Tunisia, was split into three parapatric species—*C. bicolor*, *C. viatica*, and *C. savignyi*—using mtDNA and the content of the Dufour’s gland (Wehner et al., 1994; Knaden et al., 2005). Similarly, *C. niger* from Israel was split into two species, *C. niger* (sensu stricto) and *C. holgerseni* (Collingwood and Agosti, 1996). While the contents of Dufour’s gland are somewhat similar between these species (Nei chemical distance = 0.85, i.e., 85% similarity) their cuticular hydrocarbon profiles are completely different (Nei distance 0.33, always higher than 0.90 between colonies of one species), indicating that they are clearly different species (Lenoir et al., unpublished data). Certain Iberian species were included in a phylogeny of slave-making ants, in which *Cataglyphis* species grouped together with *Rossomyrmex* and their slave *Proformica*. This relationship with *Proformica* was confirmed by larger genetic analyses (see the most recent tree in Boomsma et al., 2009).

The endemic species *C. floricola*, from Andalusia, appears to be ancestral to this group but the low bootstrap value indicates that more species are needed in order to confirm this (Hasegawa et al., 2002). *Cataglyphis* “*cursor*” is present throughout the northern region of the Mediterranean and was previously considered as a species with many subspecies. However, cuticular hydrocarbon analyses from France and Spain (Nowbahari et al., 1990) revealed that the Rhone Valley forms a border between two very different forms, confirming the old descriptions by Bondroit (Bondroit, 1918): *C. cursor* to the east of the Rhone and *C. piliscapa* to the west, up to Barcelona in Spain.

Another population, which is probably a valid species yet to be named was found in the Sierra Mountains north of Madrid. *Cataglyphis cursor hellenica* can also be considered a valid species, as proposed by Agosti (1990) and confirmed by its distinct cuticular hydrocarbon profile (A. Lenoir, unpublished data). Thus, all the subspecies of *C. cursor* probably constitute distinct species.

What speciation mechanisms may have been involved here? *Cataglyphis* ants offer a good model for speciation because in many species females are flightless. This reflects the classical parapatric speciation by isolation similar to that of Darwin's finches: the Rhone is a large river and its valley is irrigated, constituting a barrier for flightless females. The Madrid Sierra population became isolated at the end of the last glaciations and evolved independently. Another example comes from the endemic species *C. floricola*, from the Guadalquivir estuary (Doñana National Park, Andalusia, southern Spain), which appears to have arrived from Morocco and become isolated after the Straits of Gibraltar opened (Tinaut, 1993; Dahbi et al., 1996). Two color morphs of *C. floricola* were considered as a single species with regard to morphological characters (Tinaut, 1993) but preliminary genetic analysis now seems to indicate that they are two species (F. Amor and J.A. Galarza, unpublished data). Extensive work on *Cataglyphis* phylogeny using both hydrocarbon profiles and DNA analyses is now underway. Using the new tools it will be interesting to look at the divergence between species from the northern and southern Sahara.

As Darwin argued, natural selection drives the origin of species, and two broad categories of selection are known: ecological and mutation-order (see review in Schluter, 2009). Wehner et al. (1994) hypothesized that *Cataglyphis* originated in the arid regions of central Asia and spread along two routes, the northern (*cursor* group) and the southern (*bicolor* and *niger* complexes) routes into North Africa. Hence, *Cataglyphis* ants offer good models for ecological speciation that is linked to aridity gradients, as, for example, the substantial north-south displacements in North Africa and the Sahara.

#### 4. Reproduction strategies

The near-ubiquity of sexual reproduction has long been considered a paradox because sexually-reproducing individuals transmit only half of their genome whereas asexual reproduction permits the transmission of twice the number of genes (Maynard Smith, 1978). The possible disappearance of sex and the evolution of parthenogenesis are major questions in evolutionary biology. While the ant genus *Cataglyphis* has long been the focus of many behavioral and ecological studies, their mating system and reproductive strategies are only beginning to be studied. Detailed analyses of the population and colony genetic structure have been done for only a few species: *C. cursor* (Pearcy et al., 2004; Clémencet et al., 2005; Percy et al., 2006; Hardy et al., 2008), *C. mauritanica* and *C. bicolor* (Knaden and Wehner, 2006), *C. sabulosa* (Timmermans et al., 2008), and *C. livida* (Timmermans et al., 2010). Population structure and mating systems in other *Cataglyphis* species (e.g., *C. savigny*, *C. niger*, *C. hispanica*) are now under study. Overall, these studies have revealed a unique blend of biological traits, regarding (1)

queen number and replacement, (2) dispersal strategy, (3) queen mating frequency, (4) the conditional use of sexual and asexual reproduction by queens for the production of non-reproductive and reproductive offspring, respectively, and (5) worker reproduction by both arrhenotokous and thelytokous parthenogenesis.

#### *Number of queens per colony and turnover*

Species, and sometimes populations, may differ greatly in the number of breeding females per colony. A combination of field observations and genetic analyses indicates that *C. cursor*, *C. sabulosa*, *C. livida*, *C. bicolor*, *C. savignyi*, and *C. hispanica* are strictly monogynous (single-queen colonies), whereas *C. niger* and *C. mauritanica* are polygynous (multiple-queen colonies). In some species, however, social structure may also vary across populations. For example, in southern Spain the social structure of *C. velox* varies from single-queen colonies to multiple-queen colonies, according to populations (A. Tinaut and A. Lenoir, pers. observ.). Facultative polygyny (i.e., the coexistence of single- and multiple-queen colonies in a given population) has not been reported in the genus.

Queen replacement is a common phenomenon in the monogynous *C. cursor*. In this species, workers have retained the ability to produce both haploid (male) eggs by arrhenotokous parthenogenesis and diploid (female) eggs by thelytokous parthenogenesis (see below). It has been suggested that thelytokous parthenogenesis in *C. cursor* might have been selected in order to counter high queen mortality and, originally, to allow workers to replace the queen when she dies (Lenoir and Cagniant, 1986; Lenoir et al., 1988). In line with this hypothesis, genetic analyses indeed revealed that a high proportion of colonies are headed by worker-produced queens. Using genetic models, Pearcy et al. (2006) estimated that in their study population more than 60% of the colonies are headed by queens that were produced by workers, suggesting that a queen's lifespan should be relatively short in this species.

#### *Dispersal strategy*

In ants, characteristics of mating and dispersal behaviors are usually tightly connected to social structures (Bourke and Franks, 1995; Crozier and Pamilo, 1996; Ross, 2001). Monogyny is typically associated with large nuptial flights in which sexuals mate away from the nest, and there is extensive queen dispersal and independent colony founding by queens (i.e., with no assistance from workers). In contrast, polygyny often coincides with a lack of nuptial flights, mating close to or even within the natal nest, limited dispersal of mated queens, and dependent-colony founding (i.e., with the help of workers) by budding or fission. In a budding process, the new colony maintains links with the mother colony, whereas in fission the new colony progressively separates from the mother colony but, as the two daughter colonies are related, they do not display high levels of aggression (Nowbahari et al., 1990). In fission, young mated queens leave the mother nest with adult workers and brood to initiate new colonies nearby, resulting in a strong pattern of isolation-by-distance. In line with these syndromes, in the polygynous *C. mauritanica* and *C. niger* colonies, reproduction by fission and populations is

genetically structured, whereas in the monogynous *C. sabulosa*, *C. livida*, *C. bicolor*, and *C. hispanica*, colonies are founded independently and no pattern of isolation-by-distance occurs (Knaden and Wehner, 2006; Timmermans et al., 2008, 2010; L. Leniaud and S. Aron, unpublished data). Interestingly, although colonies of *C. cursor* are strictly monogynous, young queens mate close to their natal nest and colony reproduction proceeds by fission (Lenoir et al., 1988; Lenoir et al., 1990; Percy and Aron, 2006). Consistent with colony fission, comparison of population differentiation in mitochondrial and nuclear DNA markers (Clémencet et al., 2005), and kinship-distance relationships (Hardy et al., 2008) reveals a strong local population genetic structure associated with a sex-biased gene flow with reduced, very small-scale female dispersal in this species.

Limited dispersal of reproductive females is expected to enhance competition for food sources and/or nest sites among related individuals (*local resource competition* or LRC; Clark, 1978). LRC predicts an association between productivity and sex allocation, with more productive colonies investing proportionally more in male production (Frank, 1987). This is because when related queens compete, the fitness return through females decreases with increased investment in sexuals relative to the fitness return through males. Local resource competition was found to be a primary determinant of colony sex ratio in *C. cursor*. This species shows strong male-biased sex ratios at both the colony and population levels, and the male bias significantly increases with colony size. More importantly, investment in males, but not in females, is positively correlated with total investment in sexuals (Percy and Aron, 2006).

#### *Queen mating frequency*

Ants exhibit a wide range of mating systems, from obligate monoandry to extreme polyandry (Hughes et al., 2008a,b). However, most species are monoandrous or show facultative low polyandry (<2 effective mates). Higher levels of polyandry appear to be restricted to only a few genera. This is the case in the genus *Cataglyphis*, where multiple mating by queens seems to be the rule. Queens of *C. cursor* mate with 2–8 different males, with an average effective mating frequency of  $M_{e,p} = 3.8$  (Percy et al., 2009). Interestingly, field observations indicate that queens repeatedly leave the mother nest to mate with nearby males, calling them in a stereotyped posture (sexual calling behavior with a probable emission of pheromones) and then reenter the nest (Lenoir et al., 1988). The fact that queens actively seek to mate several times strongly suggests that polyandry represents a valuable increase in their fitness. Multiple mating was also reported in *C. sabulosa* and *C. livida*, where queens mate with 1–5 males ( $M_{e,p} = 2.3$ ) and 2–8 males ( $M_{e,p} = 3.4$ ), respectively (Timmermans et al., 2008, 2010). An even higher level of polyandry occurs in the monogynous species *C. savigny*, in which queens can mate with up to 14 males ( $M_{e,p} = 9.7$ ) (Leniaud et al., in prep.). These data confirm that when multiple species of the same genus are analyzed, they almost always fall into the same mating category, in the present case exclusively that of multiple mating (Boomsma et al., 2009).

Multiple mating has long been considered an enigma in evolutionary biology, because mating is assumed to be associated with energetic cost to females, as well as increased risk of predation and transmission of sexual diseases (Daly, 1978; Chapman

et al., 2003). In social insects, polyandry of queens has an additional cost because it is expected to weaken social cohesion by lowering within-colony relatedness and, hence, indirect fitness benefits from kin selection. Understanding the adaptive significance of multiple matings by queens has been the focus of a large number of empirical and theoretical studies. Both genetic and nongenetic hypotheses were suggested to account for the evolution and maintenance of polyandry (reviewed in Crozier and Fjerdingstad, 2001; Brown and Schmid-Hempel, 2003; Boomsma et al., 2005). Three such hypotheses were tested for the ant *Cataglyphis cursor*: the “sperm limitation” hypothesis, the “diploid male load” hypothesis, and the “multiple mating for genetic variability” hypothesis. However, the findings to date do not support any of them. The “sperm limitation” hypothesis suggests that multiple mating by queens may have been positively selected to achieve a greater supply of sperm for maintaining large and long-lived colonies (Cole, 1983). Contrary to the predictions of this hypothesis, there is no association between colony size and queen mating frequency; mating with only 2 or 3 males allows queens to store enough sperm to fill their spermatheca, and the amount of sperm stored by each queen does not increase with additional matings (Pearcy et al., 2009). Moreover, the amount of sperm stored has been considered as a potentially limiting factor, primarily in species with very large and long-lasting colonies. This does not apply to *C. cursor*, in which colonies are quite small, usually comprising hundreds of workers, and queens have a short life expectancy. Similar results were reported in *C. sabulosa*, in which colonies rarely exceed 300 individuals and no association was found between colony size and queen mating frequency (Timmermans et al., 2008).

The “diploid male load” hypothesis states that polyandry would have been selected for in order to reduce the variance in production of diploid males (Crozier and Page, 1985). Production of diploid males exerts particularly high fitness costs on colonies because such males are usually either sterile or produce sterile, triploid female progeny. In addition, multiple mating reduces the costs associated with mating with diploid males. Diploid males were rare, or even absent, in most populations of *C. cursor* (Pearcy et al., 2009) and *C. sabulosa* (Timmermans et al., 2008) that were sampled so far. However, mature diploid males reportedly occurred in a single population of *C. cursor*, where they produced triploid female progeny (C. Doums, personal communication). One cannot entirely exclude the possibility that polyandry was selected for by the queens in order to circumvent the costs of mating with, or of producing, diploid males. However, it seems unlikely that this hypothesis can account for the high level of queen mating frequency in this species.

Finally, the “multiple mating for genetic variability” hypothesis assumes that increased genetic diversity within colonies results in more polymorphic workers and facilitates division of labor (Crozier and Page, 1985). Recent tests of this hypothesis in *C. cursor* showed that increased genetic diversity within colonies does not result in more polymorphic workers, and task performance is not correlated with patriline (Fournier et al., 2008). Interestingly, different results were reported by Clémencet et al. (2007), who showed a positive association between mean worker size and colony level of polyandry in *C. cursor*. This finding suggests that genetic factors may indeed affect individual size



but their influence on body size is not always expressed, possibly because under some circumstances environmental factors override these factors.

Alternative hypotheses seem particularly relevant to account for polyandry in *Cataglyphis* ants. First, the “polyandry versus parasites” hypothesis states that increased genetic diversity within colonies enhances resistance to pathogens (Hamilton, 1987; Sherman et al., 1988; Keller and Reeve, 1994). This hypothesis may prove especially pertinent to scavenger ants such as *Cataglyphis*, where workers are potentially exposed to the various pathogens developing on dead arthropods. Second, according to the ‘polyandry for social harmony’ hypothesis, an increase in genetic diversity within colonies is expected to favor social harmony by reducing the conflicts between queen and workers over the maternity of males (Woyciechowski and Lomnicki, 1987; Ratnieks, 1988) and females (when workers can reproduce by thelytokous parthenogenesis) (Greeff, 1996; Percy and Aron, 2006). In *C. cursor*, genetic analyses showed that workers are, on average, more closely related to their reproductive sisters and brothers ( $r = 0.62$  and  $r = 0.32$ , respectively) than to the parthenogenetic daughters and sons of other workers ( $r = 0.42$  and  $r = 0.21$ , respectively) (Percy and Aron, 2006). Multiple mating may have been selected in queens in order to force workers to rear their siblings instead of their own offspring. Both hypotheses await further studies.

#### *Sexual and asexual reproduction*

A remarkable feature of the species *Cataglyphis cursor* is that queens use alternative modes of reproduction for the production of reproductive and nonreproductive offspring (Percy et al., 2004). While workers are produced by normal sexual reproduction from fertilized eggs, new queens are almost exclusively produced by thelytokous parthenogenesis. Thus, although *C. cursor* queens do not require mating in order to produce diploid offspring, they have retained sexual reproduction in order to produce workers. By combining asexual and sexual reproduction with multiple mating for the production of each female caste, queens increase the rate of transmission of their genes to their reproductive female offspring while maintaining genetic diversity in the worker force. Increased rates of homozygosity in female offspring indicate that thelytoky is achieved through automictic parthenogenesis with central fusion (Percy et al., 2006).

Whether the ability of queens to conditionally use sexual and asexual reproduction for the production of workers and new queens is a widespread life-history trait in the genus *Cataglyphis* or is species-specific, remains unknown. To date, it has been shown that such ability is not found in either *C. sabulosa* or *C. livida*, in which new queens and workers are both produced by sexual reproduction (Timmermans et al., 2008, 2010). However, preliminary studies (Leniaud et al., unpublished data) suggest that the use of sexual and asexual reproduction for the production of the female castes occurs in other species of *Cataglyphis*, as well. Following the pioneering work on *C. cursor*, conditional use of parthenogenesis for queen production was documented in four other ant species: *Wasmannia auropunctata* (Fournier et al., 2005), *Vollenhovia emeryi* (Ohkawara et al., 2006), *Mycocepurus smithii* (Himler et al., 2009), and *Paratrechina longicornis* (Percy, unpublished data; see also Fournier and Aron, 2009). Interestingly, two of these species

are invasive pest ants. Parthenogenesis may therefore constitute one of the factors that facilitate the invasive traits.

*Worker reproduction by arrhenotoky and thelytoky*

Another characteristic of the reproductive biology of *Cataglyphis* ants lies in the fact that workers of most species have retained their reproductive potential. In particular, they possess the ability not only to produce males by arrhenotokous parthenogenesis but also, in some species, to produce female offspring by thelytokous parthenogenesis (Cagniant, 1973). In all species studied so far, worker reproduction was reported in queenless colonies only (Cagniant, 1981; Percy and Aron, 2006; Clémencet et al., 2007; Timmermans et al., 2008). In such situations, the brood laid by the workers was found to consist exclusively of haploid males in *C. livida* (Timmermans et al., 2010) and *C. holgerseni* (S. Aron, unpublished data), suggesting that workers are unable to reproduce by thelytokous parthenogenesis. Conversely, production of both male and female offspring by orphaned workers occurs in *C. cursor* (Cagniant, 1973, 1979), *C. bicolor* (probably *C. viatica*) (Dartigues and Lenoir, 1990), *C. sabulosa* (Timmermans et al., 2010), and *C. savignyi* (Leniaud et al., in prep.).

According to kin selection theory (Hamilton, 1964), workers should forgo direct reproduction if this is balanced by fitness benefits from raising related offspring and maintaining an efficient and productive colony (Hammond and Keller, 2004). Based on relatedness, worker reproduction in monogynous colonies is favored when the queen is singly- or doubly-mated, as workers are on average more closely related to their sons ( $r = 0.5$ ) and nephews (males from sister workers  $r = 0.375$ , from half-sister workers  $r = 0.25$ ) than to their brothers (males produced by their mother,  $r = 0.25$ ) (Ratnieks, 1988). When the queen mates with more than two males, the mean relatedness between workers and the male offspring of other workers declines, causing workers to favor queen-produced males over worker-produced males. Similar reasoning holds true for production of female offspring by workers through thelytokous parthenogenesis. Up to two matings per queen, workers are, on average, more closely related to their parthenogenetic daughters ( $r = 1$ ) and nieces (daughters from full-sister workers  $r = 0.75$  and from half-sister workers  $r = 0.5$ ), than to sisters produced asexually by their mother ( $r = 0.5$ ). With more than two matings, the mean relatedness between workers declines, causing workers to favor queen-produced females over worker-produced females ( $r < 0.5$ ). Therefore, workers may inhibit the reproductive efforts of other workers (through worker- or egg-policing) or they may exhibit reproductive self-restraint (Ratnieks, 1988; Wenseleers et al., 2004). Nevertheless, worker reproduction may be favored at the individual selection level as they directly transmit their genes through a new queen. In *C. cursor*, only one queen survives and will head the colony. Aggressions were observed between workers that could be the outcome of policing, but could also reflect direct competition for reproduction between workers belonging to different patriline (Clémencet et al., 2007).

In all *Cataglyphis* species studied so far, queen mating frequency usually exceeds two events (see above), so that workers are on average more closely related to queen-derived than to worker-derived male and female sexuals. In addition to the genetic architecture

of the colonies, other factors, such as maximizing colony productivity, may also favor reproductively-restrained workers (Cole, 1986; Ratnieks, 1988; Hartmann et al., 2003). Reproduction of workers can be costly in terms of colony productivity, because the time and energy devoted to egg-laying may negatively affect brood-rearing or foraging. Moreover, in *C. cursor*, workers have a significantly lower productivity than the queens (Cagniant, 1979). Therefore, worker reproduction may be particularly detrimental in species with small colony sizes, as is the case in *Cataglyphis*. The lack of worker reproduction in queenright nests is therefore consistent with the predictions of kin selection theory both on genetic and ergonomic grounds.

It has been suggested that thelytoky is a consequence of bacterial infections, particularly by *Wolbachia* bacteria, but *Wolbachia* was not found to be responsible for parthenogenesis in ants (Wenseleers et al., 1998; Grasso et al., 2000; Himler et al., 2009). As no bacteria have been investigated other than *Cardinium*, which is associated with *Mycocepurus* ants, the role of bacteria in reproductive strategies of ants is thus largely unexplored and may hold future surprises.

Further studies on population genetics and mating strategies in other species of *Cataglyphis* should allow us to determine whether polygyny, polyandry, the conditional use of parthenogenesis for queen production, as well as worker reproduction by thelytokous parthenogenesis, originated relatively recently in the evolution of the genus or whether these are ancestral characters.

## PERSPECTIVES

We have seen that *Cataglyphis* ants have offered a heuristic model for many evolutionary problems, including providing support for the kin selection theory. Their existence as social animals that inhabit some of the harshest environments provides an excellent opportunity to study the interplay between ecology, social behavior, and reproductive strategies. Although various aspects of ecology and evolutionary biology have been studied in a variety of species, findings so far indicate *Cataglyphis* as an excellent model system. For example, the divergence in adaptation to harsh thermal conditions exhibited by the only two species of *Cataglyphis* that were thoroughly investigated to date, points to the prospect of unfolding even more diverse evolutionary routes by which such mechanisms were attained. Nestmate recognition is also a promising field; for example, it will be interesting to obtain more information on the phenomenon of rescue behavior that appears to be limited to nestmates only. No clear data exist on the nature of the signal emitted by the distressed ant: does it involve the entire cuticular hydrocarbon profile or only some of its components? Multivariate analyses revealed a small number of compounds that differ among colonies, but this is not sufficient proof and ratios may be more important than absolute concentrations (see discussion in Breed and Buchwald (2009)). The nature of the queen pheromone is also an enigma, in particular with respect to the controversy over whether it is mainly a signal or has additional primer effects (Peeters and Liebig, 2009). The sexual-calling pheromone is, likewise, not known. The already extensive work on *Cataglyphis* phylogeny using hydrocarbons and DNA needs

to be expanded. The very important discoveries that were made recently, particularly in reproduction strategies with the conditional use of sexual and asexual reproduction of queens, give rise to many additional questions. Because thelytoky of queens is not present in all species, using genetic data to understand reproduction strategies should reveal additional information on the evolution of this genus.

A note of clarification: While reviewing various papers on *Cataglyphis*, we were surprised by the problem of the gender of this name (e.g., *Cataglyphis lividus*—masculine versus *Cataglyphis livida*—feminine). According to Cagniant the name *Cataglyphis* comes from the Greek *cata* (“down”), and *glyphis* (“notch”, from the verb *glypho*, which means “sculpture”), in reference to the male genitalia. It is therefore logically feminine, as is notch in Greek (Cagniant, personal communication). Nevertheless, most researchers have used the masculine form (see papers by D. Agosti, R. Wehner, B. Bolton, and B. Taylor), and the same author has sometimes used masculine in one paper, and feminine in another one. According to Cagniant, most of the species were first described in the *Monocombus* genus (masculine), and when the transcription to *Cataglyphis* was made the gender remained unchanged. Here, we have used the species name as it appeared in the various researchers’ papers.

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