

Comparative outlook over physiological and ecological characteristics of three closely-related *Myrmica* species

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Abstract: This paper summarizes our findings on the eye morphology, visual perception, learning abilities, navigation system and recruitment strategy of three *Myrmica* species, pointing out the agreement between each species' morphological, physiological and behavioral characters as well as the accordance between these characters and each species' environmental preferences. We also draw biological generalities and report other similar studies. *Myrmica sabuleti* workers have small eyes, perceive the dimension, number of basic elements and orientation of a visual cue but do not distinguish shapes from one another. They see the colors, perceive UV light and the perspective, and adapt their vision to the light intensity. They learn odors better than visual cues and essentially use odors to navigate. *Myrmica ruginodis* workers have large eyes, distinguish shapes, small see-through forms as well as patterns of luminous points located above them. They have no olfactory memory but a very long lasting visual one. They exclusively use visual cues located above them while travelling, relying on odors only when they no longer see. *Myrmica rubra* workers have eyes of middle size and distinguish filled shapes but not hollow forms. Their olfactory and visual conditioning lead to equivalent learning in the course of time and they use all available olfactory and visual elements for navigating.

Key words: conditioning; eye morphology; navigation; odometry; recruitment; visual perception

Introduction

We have studied ethological, morphological and physiological life trends of three closely-related ant species (*Myrmica rubra* L., 1758, *M. ruginodis* Nylander, 1846, *M. sabuleti* Meinert, 1861) for 40 years. These species can easily be collected in the field and maintained in a laboratory. Their physiological and ethological abilities make them good biological models. We first studied their recruitment strategy (Cammaerts 1978) and their cycle of life (Cammaerts 1977). Later, we focused on the visual perception of *M. sabuleti* workers (Cammaerts 2004) and on their navigation system (Cammaerts & Rachidi 2009). Then we studied this species' olfactory and visual learning performances (Cammaerts et al. 2011). Later on, we analyzed the visual perception (Cammaerts 2012b, 2013a), the navigation (Cammaerts et al. 2012; Cammaerts 2012a) and the learning abilities (Cammaerts & Némeghaire 2012; Cammaerts 2012c) of *M. ruginodis* and *M. rubra* respectively.

While collecting these species in the field, we observed that they inhabited different biotopes. These three species differ morphologically only by slightly details (dimension of the spinae, shape of the antennae scape) and may be adapted to their usual environment thanks to their physiology and ethology which, indeed, rather differ. So, we examined if there was any relation between each species' usual biotope on one hand and the ethological and physiological life trends char-

acteristics we had studied, on the other hand. Doing so, our different studies appeared like pieces of puzzles which can be assembled for giving insight in these three species' physiology and trends of life. It was thus time to tidy and summarize our results, to integrate them in the actual knowledge on the subjects and to discuss several tackled topics.

The three studied *Myrmica* ants are common in Western Europe and widespread in Belgium. Generally, they inhabit different biotopes, seem to have different ecological preferences (De Koninck et al. 2012; Wegnez et al 2012; www.fourmiswalbru.be; Blatrix et al. 2013). *Myrmica sabuleti* nests in rather open and thermophilic land, sometimes in sandy regions, in not excessively lighted zones, e.g., on old coaling stations recently wooded, on steep slopes covered with herbaceous plants or in recently old quarries invaded by a few young trees and plants, where several odorous plants are growing (*Gallium mollugo*, *Trifolium repens*, *Daurus caroto*, *Cytisus scoparius*, *Fragaria vesca*). This species is not present in very old quarries where there are big trees, nor in just abandoned quarries where there are essentially stones and practically no odorous plants. *Myrmica ruginodis* generally lives in rather cold biotopes, nesting on the borders of forests, around clearings, in bocages, on woodlands. According to our observations since decades, it does not live inside dark forests but always under branches (i.e., under some canopy) where the sky is partly visible. The species never inhabits

places where there are no trees (e.g., in open land), nor where the presence of too many trees blocks the view to the sky. The species can also inhabit moorlands and grassland along rivers, nesting in partly sheltered sites, where the lighting is low. It nests in tree-trunks, in rotting-wood, under stones and in moss. *Myrmica rubra*, which life cycle has been précised (Cammaerts 1977), inhabits variable but always rather wet biotopes such as grasslands often located near bonds or rivers, open lands, borders of paths and gardens and very seldom in forests. It nests in the soil, under stones, in grass roots or in dead branches, on generally well-lighted zones, where common odorous and non-odorous plants of an intermediate size can be found, such as Poaceae, *Epilobium*, *Plantago*, *Taraxacum officinale*, *Stellaria media*, *Ranunculus acris*, *Rumex*.

Synopsis of our experimental material and methods

During our studies, we set up several experimental methods and built numerous experimental apparatus. Among others, we made corneal replicates for studying the morphology of ants' eyes (Rachidi et al. 2008); we set up a system for assessing any animal's subtended angle of vision (Cammaerts 2004); we constructed a pyramidal apparatus (Cammaerts 2008) as well as kinds of tower (Cammaerts 2012b) for analyzing ants' visual perception. We quantified ants' choices using Y mazes (Cammaerts et al. 2011) and used simple designs for obtaining differential visual as well as olfactory conditioning (Cammaerts & Rachidi 2009). Ants' navigation was examined using mazes (Cammaerts & Lambert 2009). Ants' odometry capability was revealed using tunnels (Cammaerts 2005a) and recruitment strategies were discovered essentially by obtaining ants' tracks on smoked glasses (Cammaerts 1978).

Summary of our experimental data

Eye morphology

Among the numerous ant species, the three *Myrmica* ants concerned here have eyes of comparatively middle size (Wehner 1981). Slight differences exist between the three species' eye morphometry (Fig. 1A, line 2; Rachidi et al. 2008). The eyes of *M. sabuleti* meanly contain 109 ommatidia, those of *M. ruginodis* 149 ones and those of *M. rubra* 129 ones. The eye of *M. sabuleti* is not high and has no large postero-dorsal part; it is nearly half ellipsoid. That of *M. ruginodis* is very high and presents a predominant postero-dorsal zone; it does not resemble a half ellipsoid or a half sphere. The eye of *M. rubra* is not high with not well developed dorsal part; it is rather broad and looks like a hemisphere.

Subtended angle of vision

Such an angle is the smallest angle under which an animal can perceive an element. It is not its field of vision, nor its discrimination ability. The smallest that angle is, the best is the animal's vision. This subtended

angle of vision was assessed on the basis of the foragers' maximum distance of vision. It equals 5°12' in *M. sabuleti* (Cammaerts 2004), 3°12' in *M. ruginodis* and 3°50' in *M. rubra* (Cammaerts 2011). These values (Fig. 1B, line 3) give an idea of the visual perception ability of the three species. They were retrospectively found to be in agreement with each species eye morphology (see above) and visual perception (see below).

Visual perception

Our results are schematically summarized in Fig. 1C, line 4. *Myrmica sabuleti* workers see all around themselves, among others above them. They are sensitive to the length and the width of a visual cue. They perceive the height at which a cue is located and how a cue is sloping backwards (Cammaerts 2004). The workers distinguish cues made of different numbers of elements as well as cues differently oriented being more sensitive to deviations from the horizontal than to deviations from the vertical (Cammaerts 2008). *Myrmica sabuleti* foragers are not able to discriminate filled shapes as well as hollow forms from one another except if these shapes and forms are presented with convexity (that is with their edges curved inside) (Cammaerts 2008). These workers discriminate colors from gray and colors from one another (Cammaerts 2007a). They are the most sensitive to colors *vs.* gray and are also more sensitive to colors than to shapes. They are sensitive to UV light and were proved to perceive perspective on the basis of their visual perception of UV light on one hand and of the other light (500 nm to 1,000 nm) on the other hand (Cammaerts 2007b). They adapt themselves to the light intensity. Their visual threshold becomes lower at low light intensity and higher at high light intensity. The relation between their threshold (thr) and the light intensity (i) is an exponential function: $\text{thr} = 11.62xe^{0.027x}$ with $x = i^{1/2}$ (Cammaerts 2005b). Their different sensitivities to the different wavelengths of the visible and the UV light also change with the light intensity. These sensitivities shift towards shorter wavelengths when the light intensity decreases. Essentially sensitive to yellow and blue under high light intensity, *M. sabuleti* workers become essentially sensitive to green and violet under low light intensity (Cammaerts & Cammaerts 2009). So, they adapt themselves, as summarized here below, to the quantitative and qualitative variations of the natural light which occur during the day. In nature, under very low light intensity, these ants discriminate colors from gray, no more. Then, under somewhat higher light intensity, they distinguish colors from one another. Until this time, their eyes function in a superposition mode, what does not allow a sharp perception of the visual elements. When the light intensity still increases, the ants' eyes function in an apposition mode and *M. sabuleti* workers somewhat distinguish forms and several of their characteristics (see above). Similar adaptations occur at early night when the light intensity decreases.

The visual perceptions of *M. ruginodis* and of *M. rubra* are of higher quality than that of *M. sab-*

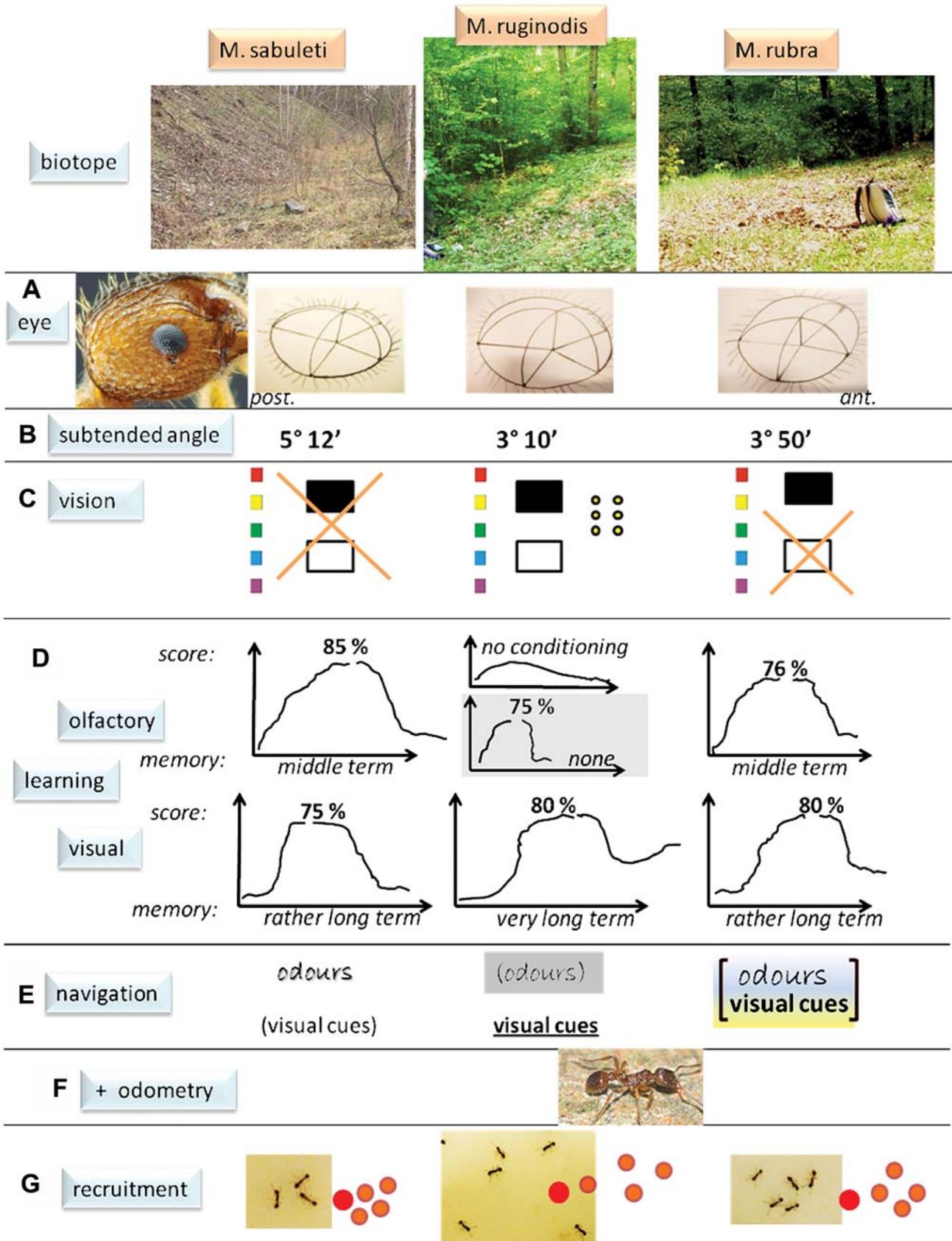


Fig. 1. Natural biotopes and schematic representation of experimental results concerning the eye morphology, subtended angle of vision, visual perception, olfactory and visual learning, orientation system and recruitment strategy of three ant species, *Myrmica sabuleti*, *M. ruginodis* and *M. rubra*. The photo of a *Myrmica*'s head, on the left of the shape of the ants' eye, has been made by Ignace (www.fourmiswalbru.be, Wegnez et al. 2012). Each line of the figure is explained in a corresponding paragraph of the 'Summary of our experimental data' section while in the abstract, the data are successively commented for each species.

uleti. The foragers of the two former ant species thus present all the visual abilities revealed in *M. sabuleti* and detain, moreover, those pointed out in each of the two species.

Myrmica ruginodis foragers distinguish filled shapes as well as hollow forms from one another. They also see transparent cues on a black background and even discriminate different patterns of small luminous points on a black ceiling. Their visual perception allows them to distinguish visual elements of the canopy as well as celestial cues (Cammaerts 2012b). These ants were proved to look above them while foraging (see below, Navigation system).

Myrmica rubra foragers discriminate filled shapes from one another but badly hollow forms, relying then essentially on the length of the perimeter of the form. The visual perception of this species is thus of higher quality than that of *M. sabuleti* but is weaker than that of *M. ruginodis*. In fact, they are unable to efficiently discriminate elements which are less obviously different than are two different filled shapes (Cammaerts 2013a). These ants look all around them, above and in front of them (see below, Navigation system).

Olfactory and visual learning

Such capabilities are generally studied on foragers living in their colony (Howard & Lawrence 1996) or on isolated and harnessed workers (Dupuy et al 2006; Josens et al. 2009; Guerrieri & D'Ettoire 2010). Working at a collective level, we detailed, as follows, the three studied species' learning characteristics (partly schematized in Fig. 1D, line 5).

Myrmica sabuleti foragers rather rapidly learn an odour and have a rather short-term olfactory memory. Their olfactory sensitivity and/or response ability are stronger at early night and weaker during the day, this in the laboratory, at constant light intensity and being so native. When these ants have to associate several odours to their food site, they consider and learn each odour separately (e.g., not globally, not as a group of odours) and can learn up to ten different odours. After a latency period, *M. sabuleti* workers slowly memorise a visual cue. They also slowly forget a memorised visual cue and retain 10% of their learning, having so a rather long-term visual memory. These ants' visual sensitivity and/or response ability are stronger during the day and weaker at early night this having once more been demonstrated in the laboratory, under constant light intensity and being so also a native capability. After having been trained to find their food near several visual cues, these ants give entire responses in the presence of all the cues as well as correspondingly reduced responses in the presence of only parts of the cues. They thus see all the visual cues globally, as a whole picture, and show only a fraction of their performance when confronted with each single visual cue (Cammaerts et al. 2011). *Myrmica ruginodis* foragers never acquire olfactory conditioning at a usual light intensity (300–500 lux). In darkness, they are very quickly olfactory conditioned but lose their learning as soon as

no more trained. When trained a second time in darkness, *M. ruginodis* foragers again become very quickly olfactory conditioned but not better than after their first training and once more lose all their learning as soon as no more trained. They have thus no – or at least nearly no – olfactory memory and associate odours to the presence of food only in darkness and only while the odours surround the food. These foragers slowly learned visual cues and also slowly lose such learning. If trained a second time, they acquired their learning more quickly, more slowly apparently forget it and then recover and keep permanently (at least during several months) 75% of the learning. They have thus a very long lasting visual memory (Cammaerts & Némeghaire 2012). As for the species *M. rubra*, the foragers could acquire olfactory as well as visual conditioning, the kinetics of these two conditionings differing. They acquired olfactory conditioning in 10 h, reached a score of 76% and lost it in 8–9 h keeping about 5.7% of it. When trained a second time, they acquired olfactory conditioning in 4h, reached a score of 85% and lost it in 18 h keeping 10% of it. This reveals a middle term lasting olfactory memory and an increase of the remembering in the course of successive conditionings. These ants acquired a visual conditioning for the first time in 12 h, reached a score of 80% and lost it in 20–22 h, keeping 10–12% of it. When trained a second time, they acquired visual conditioning in 9–10 h, reached a score of 82.5% and lost it in 30–32 h, keeping 15% of it. This points out a rather long lasting visual memory but the visual remembering does not largely increase in the course of successive conditionings (Cammaerts 2012c). *In fine*, thanks to repeated olfactory and visual conditionings, *M. rubra* foragers acquire similar remembering of olfactory and visual encountered cues. This is consistent with our results on this species' navigation system (see below).

Navigation system

This trend is schematically presented, for each species, in Fig. 1E, line 6. We firstly elucidated the travelling system of *M. sabuleti* (Cammaerts & Lambert 2009; Cammaerts & Rachidi 2009). Differentially conditioned to two different visual cues, foragers of this species can find their way in a maze duly provided with the learned cues. Similarly, differentially conditioned to two odors, these ants can negotiate their way in a maze duly provided with the odors. When confronted with the two kinds of cues, *M. sabuleti* foragers primarily use odors to travel. They continue to respond to obsolete visual cues for a time but soon stop responding to no more correct odorous elements; this have been, later on, explained by the species' olfactory and visual memory (see above, Olfactory and visual learning). The foragers of *M. ruginodis* (Cammaerts et al. 2012) find their way in a maze provided with previously learned odorous as well as visual cues. They respond exclusively to the upper bent part of the visual cues and not to the front part of these cues: they thus look above them while foraging. In mazes provided with olfactory and visual

cues set in confrontation, *M. ruginodis* foragers only respond to the visual ones, neglecting the odorous ones, even if the visual cues are obsolete. In darkness, they rely on odors to find their way but soon stop to respond to obsolete olfactory cues. This was later on explained by the species' lack of olfactory memory (see above, Olfactory and visual learning). *M. rubra*, also finds its way in mazes provided with learned olfactory or visual cues (Cammaerts 2012a). The performances of these foragers are higher for olfactory cues at low light intensity and higher for visual cues in high light intensity. In the presence of the two kinds of cues set in confrontation and at a common light intensity, these workers cannot find their way, hesitating in front of the two kinds of cue, one being correct, the other being wrong. They thus rely similarly on the two kinds of cues, the olfactory and the visual ones. This is in agreement with the species' olfactory and visual learning (see above, Olfactory and visual learning).

This subject, 'ants' navigation', examined by many researchers, is debated in the 'Discussion' section.

Odometry

Foragers of *M. rubra* were shown to be able to estimate the distances they travel by odometry, in the absence of any cues (Cammaerts 2005a; Fig. 1F, line 7). We presume that foragers of the two other studied species can also use odometry to help them in travelling. Such a help for navigating has also been found in other ant species (Wolgemuth et al. 2001; Wittinger et al. 2006).

Recruitment strategy

In general, ants recruit nestmates thanks to tandem running, or group or mass recruitment (Passera & Aron 2005). We found that the foragers of the three studied species use group recruitment strategy. After having found food, they return to their nest laying down a trail. In their nest, they 'invite', contact congeners, then come back onto their trail emitting some amount of their attractive Dufour gland content. Group recruitment thus occurs (Cammaerts-Tricot 1974a, b; Cammaerts 1978). Slight differences exist between the species (Cammaerts & Cammaerts 1980; Fig. 1G, last line). In *M. sabuleti*, the recruited ants are not very numerous and moved near the recruiting ant, the group being rather small. In *M. ruginodis*, recruited ants are rather distant from one another and form a long, broad group behind their leader. The latter species often relocate its nest in order to always inhabiting where canopy and some sky are visible (personal observation). As for *M. rubra*, recruited ants form group of middle size, e.g., longer and broader than those of *M. sabuleti* but not as long and broad as those of *M. ruginodis*.

For the three studied species as well as for other ones, the intensity of the recruitment behavior (e.g., trail depositing, congeners inviting) depends on the food quality (Cammaerts 1978), quantity (Hantgartner 1970) and distance from the nest (Devigne & Detrain 1999).

Discussion

In the course of our studies, some apparent discordances between results appeared and were later on cleared. For instance, in a first time, we showed that *M. sabuleti* workers use visual cues to navigate (Cammaerts & Lambert 2009). During these experiments, the ants had no olfactory cues at their disposal. Thereafter, we gave olfactory and visual cues to *M. sabuleti* workers and found that these ants primarily use olfactory elements to navigate. At that time, we knew the visual perception abilities of *M. sabuleti* workers, but not those of *M. ruginodis* and *M. rubra*. So, we could not evaluate the relative quality of *M. sabuleti* workers' vision. Several years later, we discovered the excellent visual perception of *M. ruginodis* workers and deduced that the *M. sabuleti* workers' one was of poor quality, and consequently explains these ants' use of odors to travel. In general, initial discordances in results are explained or corrected after additional studies on the subject. Hereafter are three examples:

1. The homing strategy of the Australian desert ant *Melophorus bagoti* Lubbock, 1883 was studied in several steps. Narendra (2007a, b) and Narendra et al. (2007a, b) showed that this ant species uses path integration but also integrates visual information as well as remembering how far it has to travel. In fact, it relies on all the elements its physiological abilities allow to detect (Schwarz & Cheng 2010a). Though the authors did not explicitly state the fact, they obviously showed that *M. bagoti* relies more or less on one or the other of its navigational method – landmark sequential memory, odometry – depending on the length of the outbound trip. Wystrach et al. (2011a) also define this efficient navigation system. Moreover, if this ant species does not exactly find its nest entrance using this information, it engages in a systematic search to find it (Schultheiss & Cheng 2011).

2. This systematic search has also been studied by Merkle & Whener (2009) in the desert ant *Cataglyphis fortis* Förster, 1850. The authors subsequently showed that ants adapt their systematic search to the distance from the nest they had foraged (the home vector) (Merkle & Whener 2010).

3. In the same way, Schwarz & Cheng (2010b) pointed out interspecific differences while studying the navigation system of the two desert ants, *C. fortis* and *M. bagoti* which inhabit different biotopes. The latter species, nesting in visually rich environment, learn visual cues more efficiently. More recently, Wystrach et al. (2011b) went a step further, somewhat modifying previous affirmations. They provided *M. bagoti* ants with a huge artificial landmark located right near the nest entrance to find out whether navigating ants focus on such a prominent visual landmark for homing guidance. When the landmark was displaced by small or large distances, ant routes were affected differently and certain behaviors appeared inconsistent with the hypothesis that guidance was based on the landmark only. Instead, comparisons of panoramic images

recorded in the field, encompassing both landmark and distal panorama, could explain most aspects of the ant behaviors.

The observations and deductions made by Wystrach et al. (2011b) are in agreement with the fact we pointed out while examining the collective operant conditioning of *M. sabuleti* foragers (Cammaerts et al. 2011). These ants learn and memorize a visual cue considering it not alone or independently from other visual cues but among such other cues, as a part, an element of the totality of perceptible visual cues. On the contrary, these workers memorize an odor separately from other perceived ones, not in addition (mixed) to several other odors.

Other ant species could be mentioned as for concordance between perception abilities, learning performances and travelling behavior. Here are three examples:

1. *Cataglyphis* spp. uses and memorizes visual cues according to a snapshot or a sketchmap models (Passera & Aron 2005). It can use celestial cues (Whener 1997), polarized light (Whener 2003), sun compass and odometry (Wehner 2009). It complementarily uses odors while travelling (Wolf & Wehner 2000), and uses odors as an additional cue for finding its nest (Steck et al. 2009). In fact, these ants use together visual and olfactory landmarks in an optimum combination (Steck et al. 2011).

2. *Gigantiops destructor* (F., 1804), which has very big eyes and nearly never uses odors, can remember performed locomotion reactions (Macquart et al. 2006), memorize sequences of visual cues (Macquart & Beugnon 2007) and integrate them into pathways (Schatz et al. 1999). It also memorizes geometry and several features of its environment (Beugnon et al. 2005; Wystrach & Beugnon 2008). It primarily uses its vision and learns landmark sequences to navigate (Wystrach et al. 2011a). *Gigantiops destructor* can also use the panoramic skyline to find its way (Schwarz et al. 2011), the complementary importance of landmarks and panoramas having been demonstrated by Wystrach et al. (2011b).

3. *Melophorus bagoti* has a remarkable homing behavior essentially made of path integration (Narendra 2007a, b). It also relies on odometry (Narendra et al. 2007a) and on memorized landmarks (Narendra et al. 2007b), and relies more on one or the other of these two systems depending on the distance it has travelled from the nest (Schwarz & Cheng 2010a). Path integration leads to some uncertainty and this ant exhibits a typical research behavior for finding entrances, when having reached the vicinity of its nest (Schultheiss & Cheng 2011).

From our results and data gathered from literature, we can deduce general characteristics on learning performances and navigation system that could be applied to any ant and other animal species. Here are four of them. The learning performances observed in a species depend on this species' perception abilities, of course, but also on the conditions occurring dur-

ing the learning process, e.g., the lighting, the temperature, the time o'clock of the day, and probably the animals' motivation. As examples, *M. sabuleti* foragers better visually learn during the day and better olfactory learn during the night; the visual learning performance of *M. rubra* workers decreases when the light intensity decreases, while their olfactory learning score then increases; *M. ruginodis* ants do not take odors into account under normal light intensity. The use of learned cues (or any other learned behavior) depends on the environmental conditions. For example, *M. rubra* workers use more their olfaction or their vision depending on the light intensity. In general, what is quickly learned is quickly forgotten and what is more slowly learned is remembered during a longer time. This has an impact on field – the animals are more incline to memorize long lasting elements – and on experimental results – the training time period largely affects the resulting learning. When an animal is able to learn something, its remembering score increases in the course of successive learning. A better memorization could so be obtained thanks to successive learning and forgetting experiments instead of thanks to a very long but alone learning experiment. In other words, on field as in laboratory, not only the training time impacts but also the number of times the animals can be trained.

The investigations related here have been and are still continued by ongoing researches on, among others, true individual visual and olfactory conditioning (Cammaerts 2013e) as well as spatio-temporal learning in the three *Myrmica* species (Cammaerts 2013b) and in differently aged workers (Cammaerts 2013f). Observing that very young ants are unable to perform any social tasks, even basic ones such as trophallaxy, trail deposit, stinging, we approached the question of the ontogenesis of the ants' different cognitive abilities. We investigated how ants acquire kin recognition (Cammaerts & Gosset, in press), how they acquire the knowledge of their nest entrances characteristics (Cammaerts 2013c), that of their foraging area odor (Cammaerts, in press), of their trail following behavior (Cammaerts 2013d) and of their alarm reaction (Cammaerts, in press). We now aim to similarly study more “primitive” species (e.g., *Manica rubida*) with the hope to understand how could have appeared the sophisticated behavior of more “complex” species.

Conclusions

The interest of the present summary is to give an insight on the ethological and physiological life trends of three related ant species, which could contribute to explain their ecological preferences. For each three studied species, the different examined characteristics are in agreement with one another: their eye morphology is in agreement with their visual perception, this perception impacts on their learning performances, and this determines their navigation system as well as other related behavior. It also appeared that the gaps of some abilities are fulfilled by other more efficient ones. An

example, among others, is the use of odors to travel by *M. sabuleti* foragers which visual perception is of poor quality. Finally, looking retrospectively to our collecting sites, we observed a concordance between each species' sensitive and cognitive capabilities and its preferred biotope, according to ours and other authors' observations

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