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Spatio-temporal learning in three *Myrmica* species (Hymenoptera : Formicidae)

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Abstract

Spatio-temporal learning was examined in three closely related ant species by training foragers to find meat in one location in the morning and sugar water at another location in the evening, over the course of 12 days. *Myrmica sabuleti* Meinert, 1861 workers showed modest but significant spatio-temporal learning abilities : about 47% of the forager population learned when food was available at the two locations. *Myrmica rubra* (Linnaeus, 1758) workers were also able to acquire some time-place learning : 41% of the foragers who had learned the time and place of sugar delivery also learned those for the meat delivery, and 32% of the foragers having memorized the time and place of the meat delivery also remembered those of the sugar delivery. *Myrmica ruginodis* Nylander, 1846 workers more clearly demonstrated a spatio-temporal learning ability. 39% of the foragers that had memorized the time and place of the sugar-water delivery also learned those of the meat delivery while 70% of the foragers who had learned the time and place of the meat delivery also learned those for the sugar deliveries. Time-place learning thus depends on the species and the kind of food. This ability may depend on the physiological state of the colony and be influenced by the ants' motivation, the time period between training experiments as well as individuals' age and experience.

Keywords : ants, cognitive abilities, foraging, food-collection, training.

Introduction

Animals find their food by foraging in known areas in some targeted manner. Most of them can also forage on specific places and/or at times where they have previously found food, which increases their efficiency (e.g. WILKIE & WILSON, 1995 ; GOULD, 1987). *Myrmica sabuleti* can acquire spatial learning, temporal learning (CAMMAERTS, 2004a) and spatial conditioning (CAMMAERTS, 2004b). These ants can also estimate the duration of time periods (CAMMAERTS, 2010). They might thus be able to associate the place(s) and time(s) at which an event (e.g. the presence of food) occurs. Not all animals possess this time-place learning capability. Nevertheless, for example, some fish species demonstrate spatio-temporal learning (REEBS, 1993, 1996). Scavenging birds also exhibit this ability (WILKIE *et al.*, 1996). Insectivorous birds acquire time-place learning better than granivorous ones (FALK *et al.*, 1992). The pigeon *Columbia livia* also clearly demonstrates this ability (WILKIE & WILLSON, 1992 ; WILKIE *et al.*, 1994). Time-place learning has also been shown in garden warblers (KREBS & BIEBACH, 1989 ; BIEBACH *et al.*, 1994). Among invertebrates, the stingless bee *Trigona amalthea* (Olivier, 1789) demonstrates some time-place learning abilities and a combined recruitment behavior (BREED *et al.,* 2002). Another *Trigona, T. fulviventris* Guérin, 1835, can more obviously acquire spatio-temporal learning (MURPHY & BREED, 2008). The honeybee can easily acquire such learning (ASCHOFF, 1986 ; FRISCH & ASCHOFF, 1987). As for ants, studies on the topic have led to discordant results. Several researchers have shown that ants cannot acquire time-place learning. REICHLE (1943) worked on *Myrmica rubra* in the field and in the laboratory ; he concluded that these ants could learn the place where food was provided but not the time at which the offering occurred. DOBRZANSKI (1956) also did not find evidence of time-place learning in fourteen species of European

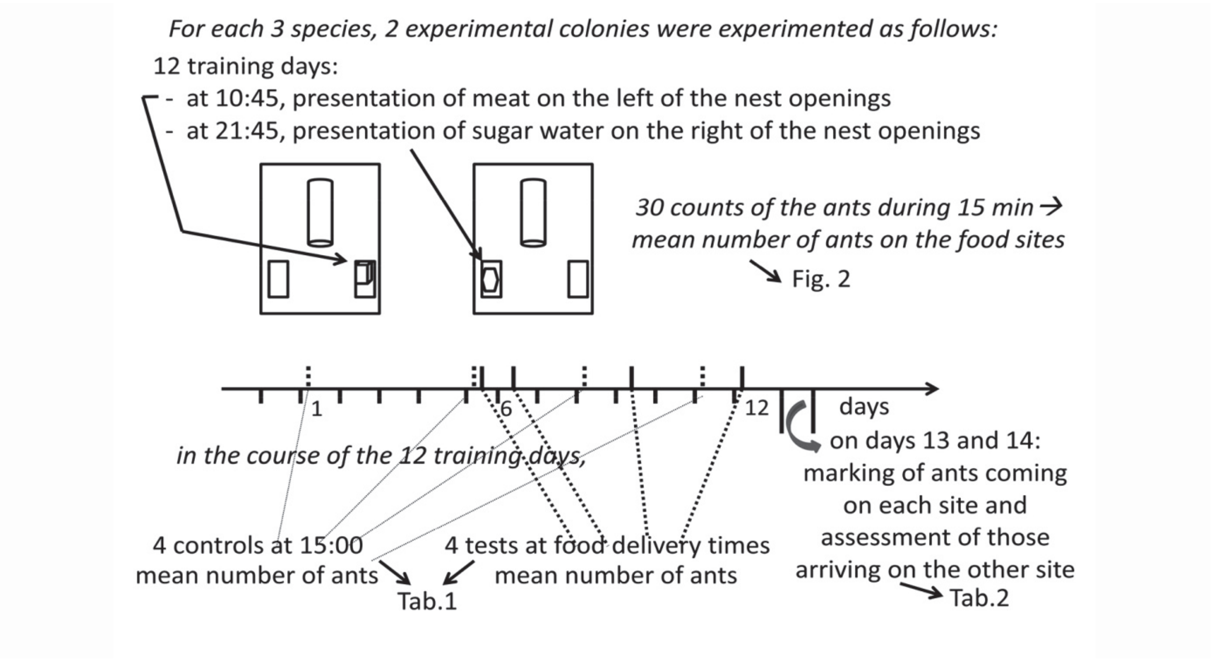

Fig. 1. Schematic view of the experimental protocol.

ants. He consequently estimated that 'time sense does not exist in ants'. On the contrary, HARRISON & BREED (1997) were able to demonstrate temporal learning in the ant *Paraponera clavata* Fabricius, 1775. Time-place learning ability has been demonstrated in the ant *Ectatomma ruidum* Roger, 1860 in successive studies (SCHATZ *et al.*, 1994 ; BEUGNON *et al.*, 1996 ; SCHATZ *et al.*, 1999). These results lead to the hypotheses that (1) ant species living in tropical areas are obliged to avoid very hot times of the day, and (2) species exploiting secretions of nectaries must visit the plants at specific times, when the secretion is at its peak. These two kinds of ants may thus be under selection to acquire spatio-temporal learning. On the contrary, literature suggests that ant species inhabiting temperate climates and/or relying on more reliable food sources (seeds, leaves, insects) do not require such an ability.

We aimed to look again at spatio-temporal learning abilities in omnivorous ant species from temperate climates because it may be advantageous to forage under comfortable temperature and lighting conditions when living in some biotopes (e.g. borders of forest, valley) or collecting some food sources (e.g. exudates of aphidae).

The biology of *M. sabuleti, M. rubra* and *M. ruginodis* is well understood. We know the morphology of their eyes (RACHIDI *et al.*, 2008), their subtended angle of vision (CAMMAERTS, 2004c, 2011), their visual perception (e.g. CAMMAERTS, 2007, 2008, 2012b), their olfactory and visual conditioning (CAMMAERTS *et al.*, 2011 ; CAMMAERTS & NÉMEGHAIRE, 2012 ; CAMMAERTS, 2012c), their recruitment strategy (CAMMAERTS-TRICOT, 1973 ; CAMMAERTS & CAMMAERTS, 1980), and their navigation system (CAMMAERTS & RACHIDI, 2009 ; CAMMAERTS *et al.*, 2012 ; CAMMAERTS, 2012a). These species live in different biotopes : *M. sabuleti* nests in open land among small odorous plants, *M. ruginodis* on the borders of forests and clearings, under branches where some sky can be seen, and *M. rubra* often on grassland. The workers of these ant species have a circadian rhythm (CAMMAERTS *et al.*, 2011), suggesting that they may be able to acquire time-place learning.

Material and Methods

Collection and maintenance of ants

The experiments were performed on two colonies (labeled 1 and 2) of *M. sabuleti*, two of *M. rubra* and two of *M. ruginodis.* Each contained a queen, brood and about 500 workers. *Myrmica sabuleti* and *M. rubra* colonies were collected at Marchin (Condroz, Belgium) ; *M. ruginodis* colonies were collected in the Aise valley (Ardenne, Belgium). They were maintained in the laboratory in artificial nests made of two to four glass tubes half-filled with water, with a cotton-plug separating the ants from the water. The glass tubes were deposited in a tray (42 x 27 x 7 cm), the sides of which were covered with talc to prevent escape. The tray served as a foraging area ; food was placed in it at given places and times. Temperature was maintained at 20° ± 2° C, relative humidity at about 80% and the lighting at 330 lux throughout the experimentation. Food, used for attempting to obtain spatio-temporal learning, was a piece of corned beef and a droplet of sugar water, each kind of food being delivered at a specific time on a glass slide (7.6 cm x 2.6 cm) at a specific place.

Experimental design and protocol

For each colony, the nest tubes were arranged so that they opened in the middle of the tray. There were two food sites, each consisting of a glass slide, set on either side of the tray and on which food was adequately delivered (Fig. 1).

We successively worked on *M. sabuleti*, *M. rubra* and *M. ruginodis*. Colonies were trained for 12 consecutive days by placing a 0.2 cm^3 piece of corned beef on the glass slide on the left of the nest tubes between 10:45 and 11:00, and 0.2 cm^3 of a saturated aqueous solution of saccharose (sugar water) on the glass slide on the right of the nest tubes between 21:45 and 22:00. The glass slide was cleaned with warm water after each training phase and returned to the nest tray, free of any food residues, at its adequate place.

During each 15 min feeding session, we counted, every 30 sec, the number of ants present on the corresponding glass slide, yielding 30 counts per session. We calculated the mean of the 30 counts for each session, each colony and each food site, and finally determined the overall mean number of ants present on each food site (Fig. 2). This allowed presuming potential time place learning by the ants.

Control experiments were performed on days 1, 5, 8 and 11 at 15:00. They consisted in counting the ants present on each empty glass slide every 30 sec during 15 min and in establishing the mean number of ants present on each food site (Tab. 1). Test experiments were performed on days 5 (i.e. after a minimum learning time period), 6, 9 and 12 at 10:38 and 21:38 by again counting the ants present on each glass slide every 30 seconds for 15 min, and establishing the mean number of ants present on each food site (Tab. 1). When a test was made, the food delivery occurred immediately afterwards.

After the experimentation, on day 13, an additional experiment was performed to check if the ants actually learned the two places and the two times. At 10:38, the ants of colony 1 coming onto the meat food site during 15 min were collected and marked with a blue spot on their gaster (Airfix® enamel). They were then put back into the middle of the foraging area and meat was provided on the appropriate glass slide until 11:08 to both colonies. At 21:38, the ants of colony 2 coming onto the sugar water site during 15 min were collected and marked in yellow. They were then put back into their colony in the middle of the foraging area. At the same time, we counted the number of marked and unmarked ants of colony 1 present on the sugar water site every 30 sec for 15 min (Tab. 2). Just after that, sugar water was delivered on the appropriate glass slides and withdrawn at 22:08. The following day at 10:45 we counted the number of marked and unmarked ants of colony 2 present on the meat site every 30 sec for 15 min (Tab. 2). At this point, the experiment ended.

Statistical analysis

The four counts obtained for a given food site had to be compared to the corresponding counts obtained for the other food site as well as to the corresponding four control counts (Tab. 1). The ants coming on each food site were the foragers of the colonies but part of them may be different from one experiment to the other. So, these four data may not be strictly independent. However, since no alternative exists, we used the non-parametric Wilcoxon test (SIEGEL & CASTELLAN, 1989). Doing so, $N = 4$ and the two highest probabilities for rejecting H_0 occur when $T = 10$ and 9 ($P = 0.0625$ and 0.125, respectively). The difference between the two compared sets of four numbers were considered as being highly significant when $T = 10$, slightly significant when $T = 9$ and not significant when $T < 9$.

Table 1. Mean numbers of ants present on the food sites during control and test experiments. For each species, the ants present on the two food sites of the two used colonies were counted four times (labeled 1 to 4, first column), this corresponding to control experiments performed on days 1, 5, 8, 11 and test experiments performed on days 5 (= i.e. after a minimum learning time period), 6, 9 and 12.

Nº of the experiment	Food site where ants were counted	Control experiment at 15:00	Test experiment	
			at 10:45 meat time	at 21:45 sugar time
M. sabuleti				
1	meat	2.7	7.8	2.1
	sugar	1.2	3.4	4.1
2	meat	4.8	12.1	3.0
	sugar	0.9	3.5	5.5
3	meat	2.7	5.6	4.0
	sugar	2.0	2.3	12.6
4	meat	4.2	9.3	4.0
	sugar	3.8	5.4	12.9
overall mean	meat	3.6	6.2	3.3
	sugar	2.0	3.6	8.8
M. rubra				
1	meat	0.5	2.8	0.4
	sugar	0.0	1.4	2.4
2	meat	0.8	2.1	0.6
	sugar	0.7	1.2	3.0
3	meat	0.5	1.0	0.5
	sugar	1.2	2.5	4.3
4	meat	1.0	1.6	0.0
	sugar	1.8	2.8	2.6
overall mean	meat	0.7	1.9	0.4
	sugar	0.9	2.0	3.1
M. ruginodis				
1	meat	1.7	2.0	0.3
	sugar	0.8	0.7	0.8
2	meat	0.8	2.3	1.1
	sugar	0.3	0.4	1.6
3	meat	0.7	3.0	1.6
	sugar	0.3	0.5	1.0
4	meat	0.3	3.4	1.0
	sugar	1.0	0.1	0.5
overall mean	meat	0.9	2.7	1.0
	sugar	0.6	0.4	1.0

Table 2. Proportion of ants, marked at a food site at a feeding time, which were subsequently found on the other feeding site at the corresponding feeding time. For each species, ants of colony 1 and 2 were marked upon arrival at the meat and the sugar sites respectively (second column). Thereafter, at the next feeding time, marked and unmarked ants present on the sugar and the meat sites, respectively, were counted and the means established (fourth column). Using the total mean number of ants present on a site (third column), the percentages of those having been marked at the other feeding site were established (fifth column).

Species	Colony (No. of marked ants)	Ants present on the other food site		
		mean No. present	mean No. marked	% marked
M. sabuleti	1 (47 on meat site)	4.6 on the sugar site	2.3	48.7
	2 (44 on sugar site)	6.9 on the meat site	3.1	44.8
M. rubra	1 (22 on meat site)	4.7 on the sugar site	1.9	41.3
	2 (12 on sugar site)	2.0 on the meat site	0.7	32.0
M. ruginodis	1 (15 on meat site)	2.8 on the sugar site	1.1	39.2
	2 (8 on sugar site)	2.1 on the meat site	1.4	69.6

Results

Training : collecting food behavior in the course of successive food presentations

The average number of *M. sabuleti* workers visiting the food sites when food was delivered increased slightly in the course of the experiment. On the meat site, it was 29.8 during the first six meat presentations and 40.8 during the last six deliveries, i.e. 1.4 times more. For the sugar water presentations, these mean numbers were 27.6 and 43.8 respectively, the ants becoming thus 1.6 times more numerous in the course of the experimentation. Such an increase did not occur for the sites where no food was delivered (Fig. 2 upper graphs).

The average number of *M. rubra* workers visiting the meat site did not increase in the course of the experiment while that visiting the sugar water site increased from 16 to 28. The number of ants visiting the sites where no food was offered did not vary during the experimentation (Fig. 2 middle graphs).

The average number of *M. ruginodis* workers coming to the food sites somewhat increased in the course of the 12 food deliveries. For the meat deliveries, their mean was 9.7 during the six first deliveries and 10.8 during the last six. For the sugar water deliveries, their mean was 5.9 and 7.1 respectively. Such an increase was not observed for the sites where no food was delivered (Fig. 2 lower graphs).

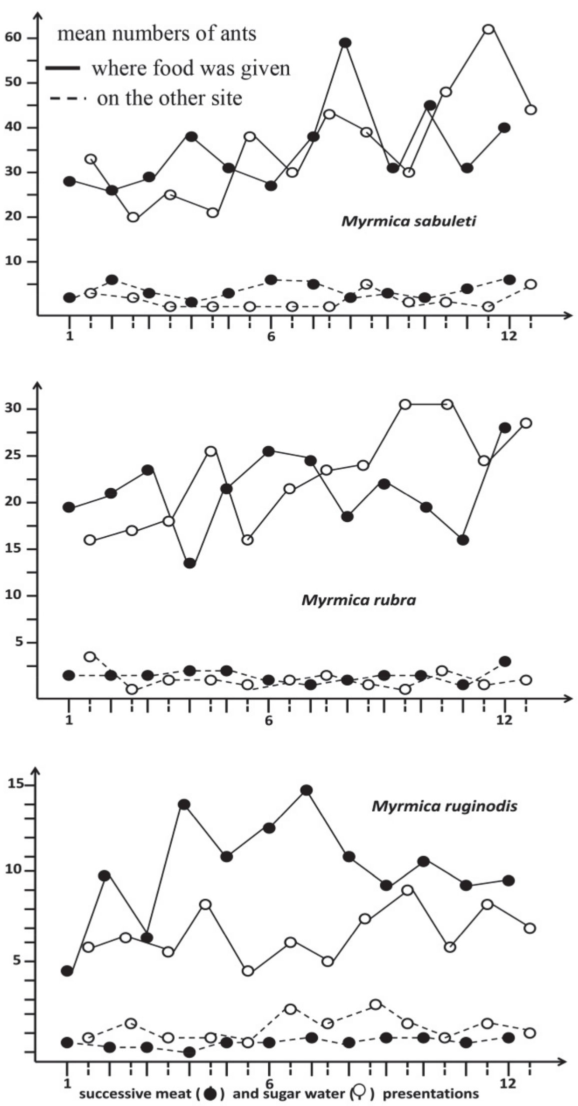

Fig. 2. Mean numbers of ants present on the meat and the sugar water sites at meat (*filled circles*) and sugar water (*empty circles*) delivery times, where food was offered (*solid lines*) and on the other empty site (*dotted lines*). These numbers, collected only during training, allowed presuming some acquisition of spatio-temporal learning by the three species.

Experiment : controls and tests

The mean number of *M. sabuleti* workers present on a food site did not increase in the course of the four control experiments. During the test experiments, the number of ants present on the meat site at the adequate time was larger than the number of ants present at the other food site (P = 0.0625) and the control value (P = 0.0625). However, the average number of ants present at meat time on the sugar site was somewhat larger than the control value (P = 0.0625). The number of ants present on the sugar water site at the correct time increased in the course of time. These numbers were larger than those of ants present at the other food site (P = 0.0625) and during the control (P = 0.0625). The number of ants present at the sugar delivery time on the meat site was similar to the corresponding control value (P = 0.5625) (Tab. 1 upper part). Some tendency of spatio-temporal learning could thus be detected in the ant *M. sabuleti*.

For *M. rubra,* in the course of the four control experiments, the number of ants present on the meat site did not increase while that of ants present on the sugar water site increased from zero to 1.8. The ants learned thus to visit the sugar water site. The number of ants present on the meat site at the correct time was not larger than that on the sugar site (P = 0.3125) but larger than the control one (P = 0.625). However, the number of ants present at the sugar site was also somewhat larger than that for the control (P = 0.0625). The number of ants present at the sugar site at the correct time was larger than the control number as well as than the number of ants visiting the meat site (P = 0.0625). Moreover, this time the ants visiting the latter site were less numerous than those seen during the control experiments (P = 0.0625) (Tab. 1 middle part). In conclusion, a tendency towards spatio-temporal learning could be demonstrated in the ant *M. rubra*.

The number of *M. ruginodis* workers present on the food sites during the control experiments did not increase. The number of ants present on the meat site at the correct time increased in the course of time. These numbers were larger than the control ones as well as than those of ants visiting the sugar site (P = 0.0625). Moreover, the number of ants then visiting the sugar site was not larger than the control one (P = 0.3125). The number of ants present on the sugar site at the adequate time were larger, but not statistically larger, than the control ones (P = 0.3125) and similar to those of ants present at the meat site (P = 0.5625), the latter number being similar to the control ones (P = 0.4375). In conclusion, *M. ruginodis* foragers have a tendency towards spatio-temporal learning.

Additional experiment : proportions of ants visiting the two food sites

If the ants had not learned the two food sites (but only one, for instance), the number of ants marked on one site, then seen on the other site, would be at the most equal to the half of the control number obtained for this food site. The different control numbers and their mean are given in Tab. 1.

As for *M. sabuleti*, 17 ants were marked while visiting the meat site at the adequate time. At the following sugar time, on the sugar site, 2.3 ants among 4.7 appeared to be marked. In the same way, 44 foragers could be marked when correctly coming on the sugar site. At the following meat time, on the meat site, 3.1 among 6.9 were seen to be marked. Consequently, ca 49% of the ants present at the sugar site had previously visited the meat site at the correct time and ca 45% of those seen on the meat site at the correct time were previously present on the sugar site at the correct time (Tab. 2 upper part). So, half of the foragers have learned the existence of the two food sites and the two times at which food could be found, having thus acquired spatio-temporal learning.

Concerning *M. rubra,* 22 ants coming on the meat site at the correct time could be marked. At the correct sugar time, on the sugar site, 1.9 among 4.7 ants appeared to be marked. So, 41% of the ants having memorized the sugar delivery also learned the meat delivery. Twelve ants could be marked on arriving on the sugar site, at the correct time. Later on, 0.7 marked ants among 2.0 were seen on the meat site at the correct time. So, 32% of the ants remembering the meat delivery were also able to memorize the sugar delivery (Tab. 2 middle part). Therefore, *M. rubra* workers were able to acquire time-place learning to a limited extent.

For *M. ruginodis,* 15 ants visiting the meat site at the correct time were marked. In the evening, 1.1 ants among 2.8 ones present on the sugar site were seen to be marked. So, about 40% of the ants having learned the sugar delivery were also able to learn the meat one. In the same way, 8 ants were marked upon arrival on the sugar site at the correct time. The following day, 1.4 ants among 2.1 ones present on the meat site appeared to be marked. So, 70% of the ants that had memorized the meat delivery were also able to memorize the sugar one (Tab. 2 lower part). In conclusion, in *M. ruginodis*, about 55% of the foragers were able to acquire spatio-temporal learning.

Discussion

Spatio-temporal learning is an advantageous ability allowing animals to know at which places and times o'clock several kinds of food are available. Until now, discordant results have been obtained about ants' ability in acquiring such a skill. We examined this capability in three *Myrmica* species inhabiting distinct biotopes in temperate climates. We found that *M. sabuleti* exhibited a tendency toward spatio-temporal learning, that *Myrmica rubra* was also able to do so but to a limited extent while *M. ruginodis* showed some capacity for spatio-temporal learning.

Spatio-temporal learning ability depends thus on the species but also on the kind of food (protein, carbohydrate, lipid ; for example, during our experimentation, ca 40% and 70% of the *M. ruginodis* foragers acquired time place learning for the meat and the sugar respectively). The ability depends therefore on the physiological state of the colony since larvae require proteins while workers preferentially consume carbohydrates. This may explain discordances between previous studies. SCHATZ *et al.* (1999) demonstrated, in the laboratory, spatio-temporal learning in the tropical ant

Ectatomma ruidum, using honey provided at time periods at which these animals would normally collect sugar in nature. The authors did not attempt to assess spatio-temporal learning with meat. Reichle (1943) and Dobrzanski (1956) also used honey for investigating spatio-temporal learning in European ants, and observed that the ants memorized the location but not the time at which food was delivered. Nevertheless, ant foragers seem to have the ability of estimating the duration of elapsed time (Harrison & Breed, 1997 ; Cammaerts, 2010). Dobrzanski (1956), Reichle (1943) and Schatz *et al.* (1999) trained ants using honey but made meat (insects) available throughout the experiment. Insects contain proteins, fat and small amounts of carbohydrates. Consequently, these ants were probably not very starved and not sufficiently motivated to learn the times of sugar delivery. In our experiment, ants received no food at all, except that provided during 15 minutes at given training times. They were thus starved and inclined to learn the food delivery characteristics. Spatio-temporal learning may therefore also depend on the workers' motivation.

Since spatio-temporal learning probably depends on the colony's level of starvation, it may depend on the duration of time between successive food presentations. A few hours may be too short. We obtained some spatio-temporal learning using intervals between feeding times of 11 and 13 hours. Schatz *et al.* (1999) used short time intervals (1 and 3.5 hours), but used delivery times (9:00–10:00, 11:00–12:00, 15:30–16:30) identical to those at which the ants collect food in nature.

In each of our experiments, the proportion of ants acquiring spatio-temporal learning was rather low (46%, 37% and 55% for *M. sabuleti, M. rubra* and *M. ruginodis* respectively). So, presumably, not all the ants demonstrated such ability. The younger and the older workers might be less able to learn in this way, while those of intermediate age might easily do so. This might also partly explain discrepancies between different studies and will be examined in a following work.

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References

Aschoff J., 1986. - Anticipation of a daily meal : a process of 'learning' due to entrainment. *Monitore Zoologico Italiano*, 20 : 195-219.

Beugnon G., Pastergue-Ruiz B., Schatz B. & Lachaud J-P., 1996. - Cognitive approach of spatial and temporal information processing in insects. *Behavioural Processes*, 35 : 55-62.

Biebach H., Krebs J.R. & Falk H., 1994. - Time-place learning, food availability and the exploitation of patches in garden warblers, *Sylvia borin. Animal Behaviour*, 48 : 273-284.

Breed M.D., Stocker E.M., Baumgartner L.K. & Vargas S.A., 2002. - Time-place learning and the ecology of recruitment in a stingless bee, *Trigona amalthea* (Hymenoptera, Apidae). *Apidologie*, 33 : 251-258.

Cammaerts M-C., 2004a. - Classical conditioning, temporal learning and spatial learning in the ant *Myrmica sabuleti*. *Biologia*, 59 : 243-256.

Cammaerts M-C., 2004b. - Visual cue generalisation and spatial conditioning in the ant *Myrmica sabuleti*. *Biologia*, 59 : 257-271.

Cammaerts M-C., 2004c. - Some characteristics of the visual perception of the ant *Myrmica sabuleti. Physiological Entomology*, 29 : 472-482

Cammaerts M.-C., 2007. - Colour vision in the ant *Myrmica sabuleti* Meinert, 1861 (Hymenoptera : Formicidae). *Myrmecological News*, 10 : 41-50.

Cammaerts M.-C., 2008. - Visual discrimination of cues differing as for their number of elements, their shape or their orientation, by the ant *Myrmica sabuleti*. *Biologia*, 63 : 1169-1180.

Cammaerts M.-C., 2010. - Estimation of elapsed time by ants. Bulletin S.R.B.E./K.B.V.E., 146 : 189-195.

Cammaerts M.-C., 2011. - Subtended angle of *Myrmica ruginodis* and *Myrmica rubra* (Formicidae, Hymenoptera). *Bulletin S.R.B.E./K.B.V.E.*, 147 : 113-120.

Cammaerts M.-C., 2012a. - Navigation system of the ant *Myrmica rubra* (Hymenoptera, Formicidae). *Myrmecological News*, 16 : 111-121.

Cammaerts M.-C. 2012b. - The visual perception of the ant *Myrmica ruginodis* (Hymenoptera, Formicidae). *Biologia*, 67 : 1165-1174.

Cammaerts M.-C. 2012c. - Olfactory and visual operant conditioning in the ant *Myrmica rubra* (Hymenoptera, Formicidae). *Bulletin S.R.B.E./K.B.V.E.*, 148 : 199-208.

CAMMAERTS M-C. & CAMMAERTS R., 1980. - Food recruitment strategies of the ants *Myrmica sabuleti* and *Myrmica ruginodis*. *Behavioural Processes*, 5 : 251-270.

CAMMAERTS M.-C. & NEMEGHAIRE S., 2012. - Why do workers of *Myrmica ruginodis* (Hymenoptera, Formicidae) navigate by relying mainly on their vision. *Bulletin S.R.B.E./K.B.V.E.*, 148 : 42-52.

CAMMAERTS M.-C. & RACHIDI Z. 2009. - Olfactive conditioning and use of visual and odorous elements for movement in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). *Myrmecological News*, 12 : 117-127.

CAMMAERTS M.-C., RACHIDI Z., BEKE S. & ESSAADI Y., 2012. - Use of olfactory and visual cues for traveling by the ant *Myrmica ruginodis* (Hymenoptera, Formicidae). *Myrmecological News*, 16 :45-55.

CAMMAERTS M.-C., RACHIDI Z. & CAMMAERTS D., 2011. - Collective operant conditioning and circadian rhythms in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). *Bulletin S.R.B.E./K.B.V.E.*, 147 : 142-154.

CAMMAERTS-TRICOT M-C., 1974. - Recrutement d'ouvrières, chez *Myrmica rubra*, par les phéromones de l'appareil à venin. *Behaviour*, 1-2 : 111-122.

DOBRZANSKI J., 1956. - *Badania nad zmystem czasu u mrowek. Folia Biologica*, Krakow, 4 : 385-397.

FALK H., BIEBACH H. & KREBS J.R., 1992. - Learning a time-place pattern of food availability : a comparison between an insectivorous and a granivorous weaver species *Ploceus bicolor* and *Euplectes hordeaceus*. *Behavioral Ecology and Sociobiology*, 31 :9-15.

FRISCH B. & ASCHOFF J., 1987. - Circadian rhythms in honeybees : entrainment by feeding cycles. *Physiological Entomology*, 12 : 41-49.

GOULD J.L., 1987. - Honey bees store learned flower-landing behavior according to time of day. *Animal Behaviour*, 35 : 1579-1581.

HARRISON J.M. & BREED M.D., 1987. - Temporal learning in the giant tropical ant, *Paraponera clavata*. *Physiological Entomology*, 12 : 317-320.

KREBS J.R. & BIEBACH H., 1989. - Time-place learning by garden warblers (*Sylvia borin*) : route or map? *Ethology*, 83 : 248-256.

MURPHY C.M. & BREED M.D., 2008. - Time-place learning in a neotropical Stingless bee, *Trigona fulviventris* Guérin (Hymenoptera : Apidae). *Journal of the Kansas Entomological Society*, 81 : 73-76.

RACHIDI Z., CAMMAERTS M.-C. & DEBEIR O., 2008. - Morphometric study of the eye of three species of *Myrmica* (Formicidae). *Belgian Journal of Entomology*, 10 : 81-91.

REEBS S.G., 1993. - A test of time-place learning in a cichlid fish. *Behavioural Processes*, 30 : 273-281.

REEBS S.G., 1996. - Time-place learning in golden shiners (Pisces : Cyprinidae). *Behavioural Processes*, 36 : 253-262.

REICHLE F., 1943. - Untersuchungen über Frequenzrhythmen bei Ameisen. *Zeitschrift für vergleichende Physiologie*, 30 : 227-256.

SCHATZ B., BEUGNON G. & LACHAUD J-P., 1994. - Time-place learning by an invertebrate, the ant *Ectatomma ruidum* Roger. *Animal Behaviour*, 48 : 236-238.

SCHATZ B., LACHAUD J-P & BEUGNON G., 1999. - Spatio-temporal learning by the ant *Ectatomma ruidum*. *Journal of Experimental Biology*, 202 : 1897-1907.

SIEGEL S. & CASTELLAN N.J., 1989. - Non parametric statistics for the behavioural sciences. McGraw-Hill Book Company, Singapore, 396 pp.

WILKIE D.M., CARR J.A.R., SIEGENTHALER A., LENGER B., LIU M. & KWOK M., 1996. - Field observations of time-place behavior in scavenging birds. *Behavioural Processes,* 38 : 77-88.

WILKIE D.M., SAKISDA L.M., SAMSON P. & LEE A., 1994. - Properties of time-place learning by pigeons, *Columbia livia. Behavioural Processes*, 31 : 39-56.

WILKIE D.M. & WILLSON R.J., 1992. - Time-place learning by pigeons, *Columbia livia*. *Journal of the Experimental Analysis of Behavior*, 57 : 145-158.

WILKIE D.M. & WILLSON R.J., 1995. - More evidence of robust spatial associative memory in the pigeon *Columbia livia. Animal Behaviour*, 230 : 69-75.