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New insight on ant colony organization

Marie-Claire Cammaerts[1,*]
27, Square du Castel Fleuri, 1170 Bruxelles, Belgium.

ABSTRACT

The social organization of a colony of the ant *Myrmica sabuleti* is defined. This colony contained six different kinds of workers differing in their linear speed, angular speed, orientation, audacity, tactile perception, aggressiveness, escaping ability, conditioning acquisition, activity, and brood caring. For each kind of ants, two ants were examined. The different kinds of ants differed in their examined biological traits. Also, the two workers of each kind slightly differed with respect to their biological traits from one another: the workers located far from the nest differing more than the workers located near or in the nest. Some cases of idiosyncrasy could be revealed. These findings are in agreement with what is generally reported about the ant colony organization, but are more precise, and more informative. The organization found herein is valid for the examined colony, at a given time, and could change over the seasons, be different for other colonies, and of course differs from that of other ant species.

KEYWORDS: aggressiveness, conditioning, division of labor, idiosyncrasy, locomotion, social life, social regulation.

*Email id: mccammaerts@gmail.com

The author is retired from the below-mentioned institution and the present work was done after her retirement.

[1]Assistant professor and researcher, retired from the Biology of Organisms Department, University of Brussels, Belgium.

ABBREVIATIONS

mm/s: millimeter per second; ang.deg./cm: angular degrees per centimeter; ang.deg.: angular degrees; n°: number; %: proportion, percentage; min or ': minute; s or '': second.

INTRODUCTION

In any group and colony, there exists naturally some division of labor depending on the age of the individuals, the young ones being not yet able to perform the most complex tasks, or having not yet the anatomical or physiological characteristics required for performing some works. In addition, some labor division can exist in societies independent of the age of the individuals, based on these individual's anatomical or physiological characteristics, and on their individual competence for accomplishing some tasks. This could ensure a better maintenance and general functioning of the society. In ants, for instance, some ants are 'scout ants', at least for some time [1]. Another example, reported in a magazine, is the fact that some ants were found to be aggressive towards an enemy while other ones were not, even if the observation was replicated. Such a difference relative to the ants' aggressiveness has also been observed by Atsarkira *et al.* [2] and Ia kovlev [3 in Reznikova, 2017].

In fact, the young individuals must learn to perform many activities, and what they learn while being young, what they experience during their first period of life, largely impact and even determine their later competences, ability to do some works, knowledge of some notion, and development of some capabilities [4]. This is true for humans (e.g., learning of music, sports, languages) of course, but also for animals (e.g., dogs, cats, horses, parrots, elephants). In ants, as an example, the young workers do not make any antennal contact, but receive several ones, and while experiencing the latter, they ‘learn’, understand the meaning of the different antennal contacts its society can use. This initial learning by the young ants of the social antennal contacts determines their future communication skill with nestmates [2]. Also, during their first or second year of life, the ants learn several notions and the accomplishing of several tasks, e.g., their nest entrance marking, their foraging area marking, their alarm pheromone, their trail pheromone and the trail following (see for instance [5-7]). All these learnings may differ between the young ants, and thus, when being adults, these ants may be able to perform tasks with difference competences, and may even present some different sensibility to different elements.

The general organization of an ant colony has been largely described in books and reviews such as [1, 8, 9]. This topic gave rise to mathematical modeling, e.g., [10]. However, there are very few experimental works which described, quantified, the behavior of the different ants of a colony with regard to the location of these individuals in the nest and the foraging area, and which led to a definite description of the ant colony organization. Moreover, the conducted experimental works were not sufficient and did not reach their aim (e.g., [11, 12]). The aim of the present work is to fill this gap, with the hypothesis that the ants’ behavior is correlated to their age, this age being evaluated thanks to the localization of the ants in their territory. The formulated hypothesis is thus that oldest ants were in outer regions of the ants’ area while younger ants were inside the nest, and that these locations could be reflected in their behavior and biological traits. The present paper reports an exploratory study investigating on this hypothesis, and provides new insight about a colony social organization.

More precisely, for investigating the division of labor which exists in an ant colony as well as the potential idiosyncrasy prevailing in such colonies, ten physiological and ethological traits were assessed in two ants present at six different places (i.e., far from the nest, not far from the nest, near the nest, at the nest entrance, inside the entrance, inside the nest), namely, the linear speed, angular speed, orientation capability, audacity, tactile perception, aggressiveness towards an alien ant, escaping ability, conditioning acquisition, activity, and brood caring. For each kind of ants, the data obtained for the two experimented ants were compared (idiosyncrasy). The data recorded for the six different kinds of ants were also compared (social structure of the colony). All this allowed defining the organization of the experimented ant colony.

MATERIALS AND METHODS

Collection and maintenance of ants

The experiments were conducted on a small colony of *Myrmica sabuleti* Meinert, 1861 collected in spring 2022 from the Aise valley (Ardenne, Belgium). It contained about 200 workers, brood and a queen. The colony was maintained in one to three glass tubes half-filled with water, the ants being separated from the water by a cotton plug. The nest tubes were laid in a tray (34 cm × 23 cm × 4 cm), whose borders were slightly covered with talcum powder to prevent ants from escaping. The tray served as a foraging area where pieces of mealworms (*Tenebrio molitor* (Linnaeus, 1758) larvae) were delivered three times per week, and where a 15% sugar water solution was permanently provided in a cotton-plugged tube. The lighting of the laboratory varied between *ca* 330 lux while working on ants and *ca* 110 lux while not doing so; the temperature equaled *ca* 20 °C, the humidity *ca* 80% and the electromagnetic field *ca.* 2 μWm^2, all these conditions being suitable for the species. The word ‘ant’ is sometimes replaced by ‘nestmates’ or ‘congeners’.

Experimental protocols

The ants moving far from the nest, those moving not far from the nest, those staying rather near the nest, those staying at the nest entrance, those being in the nest entrance, and those which were inside the nest near the brood were successively considered. For each of these ants’ location, two ants were successively observed, and ten of their biological traits were assessed: their linear speed, angular speed, orientation ability, audacity, tactile perception, aggressiveness towards an alien ant, escaping behavior, conditioning acquisition, activity, and brood caring. The experimental protocols, assessments, and analysis of the results were exactly the same as those used for examining the effects of products used by humans, or were adapted to the present experimental work. Since until now the effects of 66 products or situations used by humans have been examined, and since all the experimental methods are each time reported in publications, these methods are only briefly recalled here and the readers are referred to any of already published works, such as [13-16]. However, explanation is given for the protocols which were somewhat modified for adapting to the current situation prevailing in the present work. The assessments were here made many times on a single ant instead of being made once on several ants. Some of them were made 40 times and could be statistically analyzed; other ones were made once or a few times and therefore could not be statistically analyzed.

The ants' linear speed, angular speed, and orientation were assessed by recording forty ant's trajectories and analyzing them using an adequate software, and then establishing the median and the quartiles of the recorded values. The ant's audacity was evaluated by counting its presence on an unknown apparatus twenty times over ten minutes, and establishing the mean and extremes of the recorded numbers. The ant's tactile perception was quantified by assessing its linear and angular speeds while it walked on a rough substrate (if perceiving the uncomfortable character of such a substrate, the ant walks more slowly and sinuously as usual), and by establishing the median and quartiles of the obtained values. The ant's aggressiveness towards an alien ant was quantified by counting, in the course of a dyadic encountering lasting 5 minutes, the number of times it did nothing (level 0), contacted the opponent with its antennae (level 1), opened its mandibles (level 2), gripped the opponent (level 3), tried to sting or stung the opponent (level 4). Also, a variable 'numbers of levels 2 + 3 + 4 / levels 0 + 1' was calculated. The ant's ability to escape from an enclosure was evaluated by inserting it under a reversed glass provided with a notch (an exit) and registering the passing time before it escaped (if it could) over 12 minutes. The ant's conditioning acquisition was assessed by training it to an olfactory and visual stimulus, i.e., to seeds of lavender, set far from the nest, not far from it, near it, at the nest entrance, in the entrance and in the nest, by testing the ant in a Y-maze provided with this stimulus in one of its branches, by counting its correct responses given during 3 tests made over 12 hours (every eight hours), and finally by establishing its mean conditioning score. Since the different kinds of ants reached different levels of conditioning scores, their memory could not be compared. The ant's activity was evaluated by establishing 20 times over 10 minutes if it was active (walking, transporting a larva, making antennal contacts …) or not, and calculating the obtained 'n times being active / 20. The ant's brood caring was quantified by removing larvae from the nest, then observing if the ant found, held and transported a larva towards the nest.

All the conducted experiments could not be illustrated. However, a schema of the experimental design and a photo of each of the ten considered traits are provided (Figures 1, 2). The numerical results are summarized in Table 1 and schematized in Figure 3. Then, taken two by two, they are otherwise, graphically, presented in Figure 4.

RESULTS

All these results are summarized in Table 1 and schematized in Figure 3; photos are shown in Figure 2.

Ants far from nest

These ants walked quickly and not sinuously. The two examined ants differed with regard to such a locomotion: linear speed: $\chi^2 = 42.72$, df = 1, $P < 0.001$; angular speed: $\chi^2 = 20.31$, df = 2, $P < 0.001$. Orientation: They well orientated themselves towards a tied nestmate, but only slightly differed with regard to such an orientation ($\chi^2 = 4.17$, df = 1, $0.02 < P < 0.05$). Concerning their audacity, they soon came without hesitation on the presented apparatus, and the second tested ant was somewhat more audacious than the first one, but the difference between the two ants was not

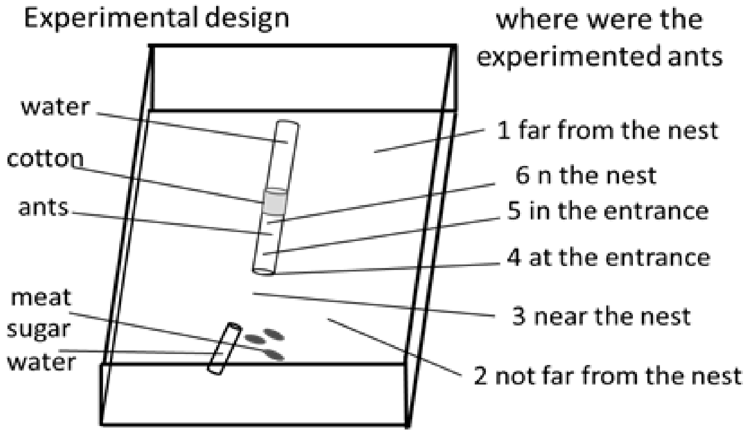

Figure 1. Schema of the design used to assess ten ethological and physiological traits of two ants located at six different places of their nest and its surrounding. Photos are shown in Figure 2, results are given in Table 1, summarized in Figure 3, and otherwise presented in Figure 4. The different kinds of ants presented quantitative differences of these traits due to their age and their social activities (what leads to define social organization). The two experimented ants of each kind became somewhat different due to their experienced events (what leads to some idiosyncrasy).

significant (N = 7, P = 0.078 what is at the limit of significance). Their tactile perception was very weak, that of the second examined ant being lower than that of the first ant. In fact, for the first ant, the statistical comparison of its locomotion on an usual area and on a rough substrate gave: for the linear speed - $\chi^2 = 33.26$, df = 1, P < 0.001 and for the angular sped - $\chi^2 = 39.30$, df = 1, P < 0.001 (so it rather well perceived the rough character of the substrate), while for the second examined ant, the comparison gave: for the linear speed - $\chi^2 = 2.25$, df = 1, 0.10 < P < 0.20 and for the angular speed - $\chi^2 = 11.43$, df = 1, P just < 0.001 (so it very poorly perceived the rough character of the substrate). Unexpectedly, none of the experimented ants showed aggressive behavior towards the presented alien ant. The numbers of times they presented the four considered levels of aggressiveness were statistically similar ($\chi^2 = 1.58$, df = 2, 0.30 v P < 0.50), and the variable ‘a’ assessing their aggressiveness equaled 0.50 for the first ant and 0.44 for the second ant. The escaping ability of the two considered ants was identical and excellent: they escaped in one minute. These ants moving far from the nest did not reach a high conditioning score. One ant gave 6 correct responses and the other 16 correct ones, the difference between them being thus high since equaling 10 correct responses, and their mean conditioning score being low since equaling 22/60 = 36.6%. These ants were very active. One ant had an activity of 1.000, and another ant had an activity of 0.900, the difference with regard to the activity between them equaling thus 1/10, and their mean activity equaling thus 0.950. They were not inclined to take care of the provided larvae. One ant did nothing during the 5 experimental minutes; the other ant took a larva in its mandibles after 3 minutes. The difference between the two ants was thus more than 2 minutes, and their mean time for caring of a larva more than 4 minutes.

Ants not far from nest

These ants walked rather quickly and not sinuously. The two examined ants did not differ with regard to their linear speed ($\chi^2 = 0.05$, df = 1, 0.80 < P < 0.90), and differed a little with regard to their sinuosity ($\chi^2 = 12.31$, df = 2, P slightly < 0.001). They well oriented themselves to a tied nestmate, and differed with regard to this trait: the second tested ant presented a better orientation than the first one ($\chi^2 = 16.31$, df = 2, P < 0.001), though the difference was not very large. Concerning their audacity, it was large and there was no difference between the two ants: N = 6, T = 14, P = 0.281. Regarding their tactile perception, each two ants perceived the rough character of the

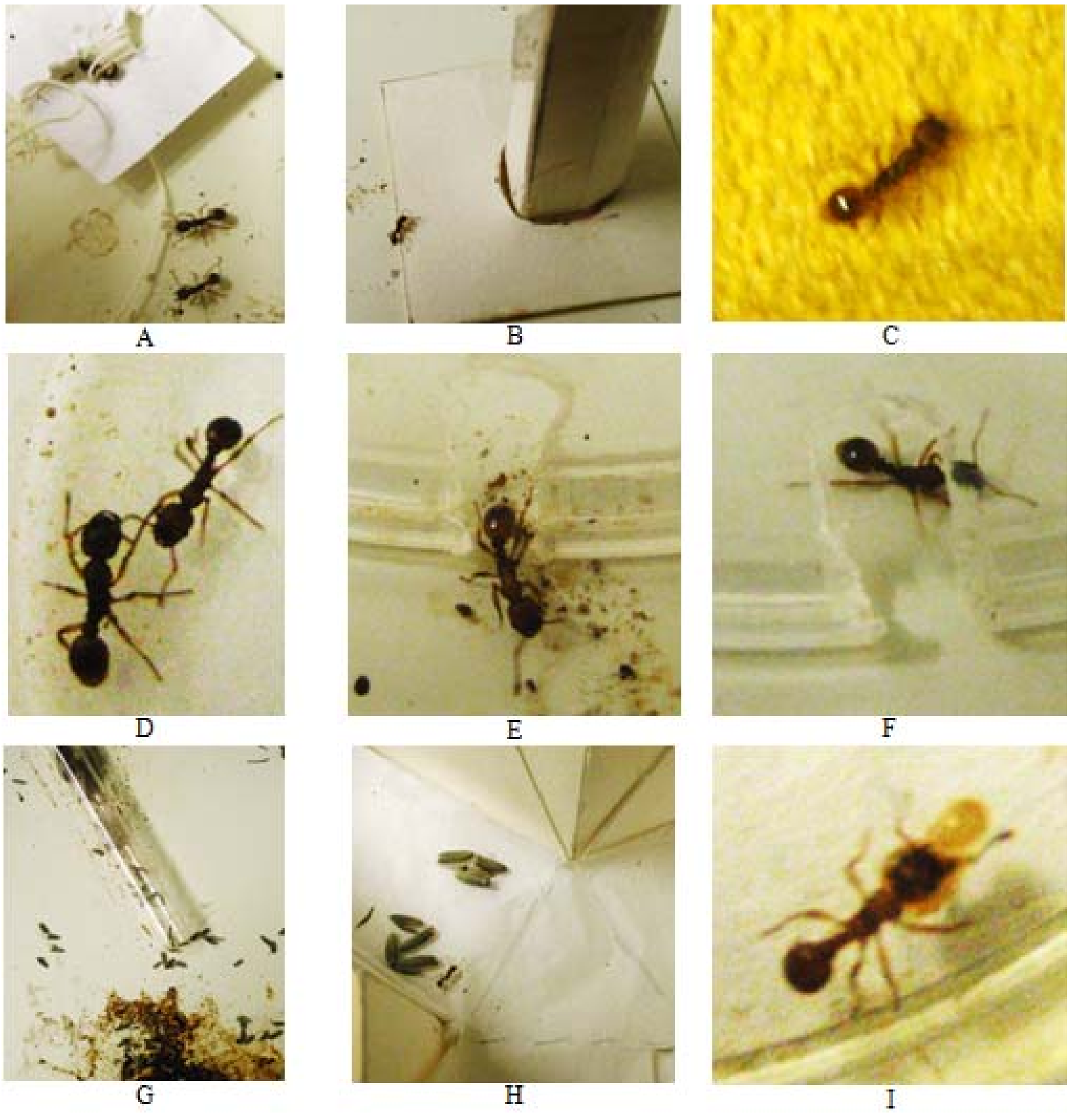

Figure 2. The experiments were so vast that only a few photos of them could be shown. The aim was the readers' visualizing of our methods. A: a tied nestmate emitting its attractive alarm pheromone. B: presentation of an unknown apparatus. C: an ant on a rough substrate. D: dyadic encountering allowing assessing an ant's aggressiveness. E, F: an ant enclosed inside a reverse cup provided with an exit and going out or not from the enclosure. G: ants' training to lavender odor. H: such a trained ant giving the correct response in a Y-maze provided with lavender in one of its branches. I: an ant holding a larva removed from the nest.

substrate, and the second examined ant did so more than the first one. Indeed, the statistical results were, for the linear speeds: first ant - χ^2 = 17.80, df = 1, P < 0.001, second ant - χ^2 = 18.46, df = 1, P < 0.001; for the angular speed: first ant - χ^2 = 14.86, df = 2, P < 0.001, second ant - 49.65, df = 2, P < 0.001 (larger value of χ^2). Each of the experimented ants did not really show aggressive behavior towards the alien ant, but very often largely opened their mandibles in front of it and incited it to go away. They similarly exhibited this behavior: the difference between the number of times they presented the four levels of aggressiveness did not differ statistically (χ^2 = 2.05, df = 2, 0.30 v P < 0.50) and the variable assessing their aggressiveness level equaled 2.00 for the first ant and 1.00 for the second one. Their escaping behavior was identical and rather good:

Table 1. Evaluation of ten biological traits of ants located at six different places in their nest and its environment. For each ant's location, two individuals were examined; they sometimes differed from one another, presenting thus some idiosyncrasy. The ants' behavioral profile differed according to their localization, and thus to their activities in the colony. Details regarding the experimental protocols and the statistical results are given in the text; the experimental design and some photos are shown in Figures 1 and 2; results are illustrated in Figures 3 and 4. Linear speed (Ls) in mm/s; angular speed (As) in ang.deg./cm; orientation in ang.deg. audacity: mean n° of ants on an unknown apparatus; aggressiveness: variable 'a' (see the text for explanation); escape ability: time (in minute) before escaping; conditioning: mean obtained score in percentage (%); brood caring: time (in minute) before transporting a larva.

Ants' localization	Linear speed	Angular speed	Orientation	Audacity	Tactile perception
far from nest	7.3 (6.6 – 8.1) 5.3 (4.7 – 5.8)	105 (78 – 124) 148 (121 – 184)	42.1 (29.4 – 56.4) 30.7 (19.9 – 48.2)	0.50 0.75	Ls: 5.6 As: 180 Ls: 5.4 As: 186
not far from nest	4.1 (3.9 – 4.7) 4.1 (3.6 – 4.6)	199 (166 – 237) 157 (134 – 174)	39.9 (28.2 – 51.0) 22.8 (17.3 – 36.7)	0.35 0.20	Ls: 3.3 As: 259 Ls: 3.3 As: 308
near the nest	2.7 (2.4 – 3.0) 2.1 (1.8 – 2.5)	270 (240 – 300) 316 (249 – 365)	64.4 (46.4 – 82.5) 62.8 (50.4 – 100)	0.25 0.15	Ls: 1.8 As: 383 Ls: 1.9 As: 371
at nest entrance	2.2 (1.9 – 2.5) 2.1 (1.9 – 2.4)	342 (308 – 382) 353 (275 – 406)	77.6 (62.3 – 98.6) 78.5 (69.3 – 94.4)	0.10 0.05	Ls: 1.5 As: 392 Ls: 1.3 As: 448
inside entrance	1.5 (1.2 – 1.7) 1.4 (1.2 – 1.5)	424 (362 – 468) 389 (312 – 506)	97.2 (76.7 – 106) 94.7 (94.7 – 114)	0.10 0.00	Ls: 0.5 As: 490 Ls: 0.5 As: 429
inside the nest	2.0 (1.0 – 4.0) 2.0 (1.0 – 3.0)	500 (442 – 630) 480 (400 – 545)	112.0 (98.0 – 126) 109.0 (94.0 – 128)	0.05 0.00	Ls: 0.9 As: 540 Ls: 0.9 As: 540
Ants' localization	**Aggressiveness**	**Escape ability**	**Conditioning**	**Activity**	**Brood caring**
far from nest	3 7 5 0 0 14 11 11 0 0	1 min 1 min	20.0% 53.0%	1.000 0.900	>5 min 3 min
not far from nest	4 7 22 0 0 8 12 20 0 0	4 min 4 min	56.6% 30.0%	0.900 1.000	>5min 2 min
near the nest	2 7 28 0 6 3 6 29 0 7	7 min 8 min	56.6% 43.3%	0.700 0.900	3 min 2 min
at nest entrance	3 10 20 0 0 3 8 18 0 8	9 min 9 min	66.6% 53.3%	0.550 0.750	1 min 1 min 30 s
inside entrance	26 15 2 0 0 27 10 2 0 0	11 min 11 min	66.6% 60.0%	0.650 0.600	30 s <20 s
inside the nest	38 5 0 0 0 36 4 0 0 0	>12 min >12 min	73.3% 70.0%	0.900 0.750	20 s 20 s

each of the two ants could escape in 4 minutes. Concerning their conditioning acquisition, it was rather bad. One of these ants walking not far from the nest gave 17 correct responses, the other one 13 ones over the 30 performed tests on each one. The difference between the two ants equaled thus 8 correct responses, and their mean conditioning score 26 / 60 = 43.3%. These ants were very

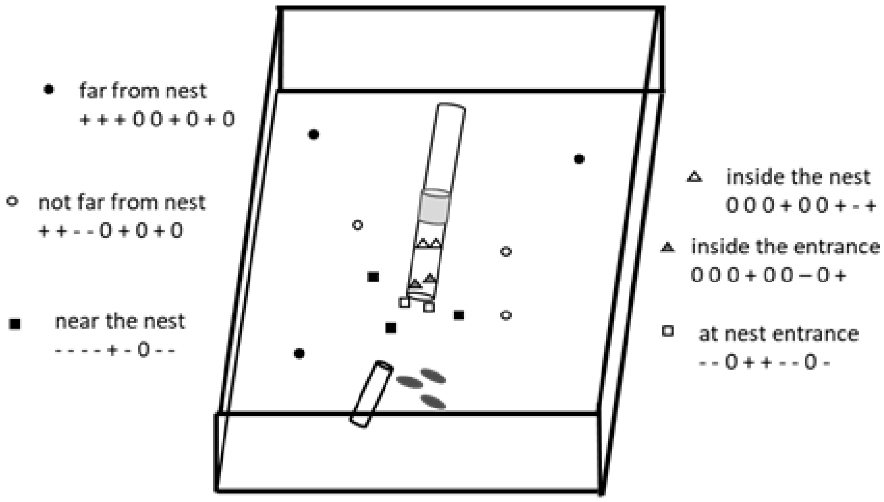

Figure 3. Results briefly schematized. For each kind of ants, three ones are represented, but only two ones were experimented. Their different successively studied traits (i.e., locomotion, orientation, audacity, tactile perception, aggressiveness, escaping ability, conditioning acquisition, activity, and brood caring) were found to be: +: large, a lot of, often; -: of middle value; 0: low, rare. A more detailed summary is given in the conclusion section, and the numerical values are reported in Table 1.

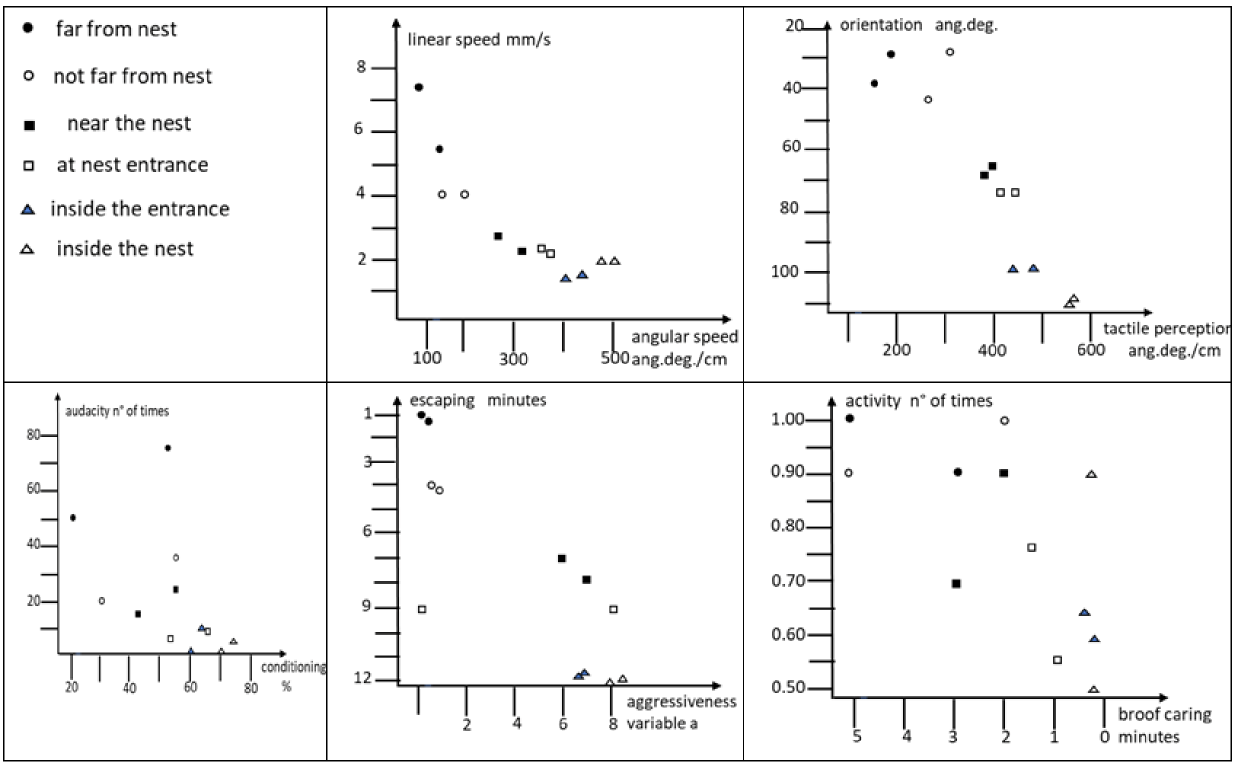

Figure 4. Another representation of the results allowing to reveal the occurrence of some idiosyncrasy among the ants; see for instance the aggressiveness of the ants located at the nest entrance. The traits which allowed to best differentiate the six kinds of workers were these workers' locomotion, orientation, tactile perception, audacity, and conditioning: the traits not allowing well to do so were the escaping and the activity.

active. Their activity equaled 0.900 for one ant and 1.000 for the other. Their mean activity equaled thus 0.950, and the difference between the two ants 1/10. These ants were not very inclined to take care of the provided larvae. One ant did nothing for 5 minutes, while the other took a larva between its mandibles after 2 minutes. Their mean time before caring of a larva was thus greater than 3 min 30 s, and the time difference between the two ants was greater than 3 minutes.

Comparison of ants far from nest and ants not far from nest

The two kinds of ants largely differed with regard to several of their biological traits, and the difference between these two kinds of ants was more than the difference found between the two examined ants of each type. Concerning the locomotion, the ants not far from nest walked more slowly (χ^2 = 69.59, df = 2, P < 0.001) and more sinuously (χ^2 = 40.60, df = 3, P < 0.001) than those present not far from the nest. On the contrary, there was no difference between the orientation of ants far from nest and that of ants not far from nest: χ^2 = 0.10, df = 1, 0.70 < P < 0.80. The two kinds of ants differed with regard to their audacity: those far from nest presenting a higher one: N = 7, T = -28 (the highest possible value, P = 0.07). Concerning their tactile perception, there was a difference between the two kinds of ants. The ants far from the nest poorly perceived the rough character of the substrate (the first examined ant perceiving it very poorly) while those not far from nest somewhat perceived this character, though the second examined ant did so somewhat less than the first one. The two kinds of ants differed with regard to their aggressiveness towards an alien ant. The mean value of the variable ‘a’ assessing this aggressiveness equaled 0.46 for ants far from the nest and 1.35 for ants not far from the nest. Also, the number of times they presented the four considered levels of aggressiveness statistically differed (χ^2 = 8.90, df = 2, 0.01 < P < 0.02), the ants moving not far from the nest being more aggressive than those moving far from the nest. Concerning the escaping behavior, the performance of ants far from nest was higher than that of ants not far from nest (the former escaped in 1 minute, the later in 4 minutes). The ant walking not far from the nest reached a higher conditioning score (43.3%) than those walking far from the nest (36.6%). Also, the difference between the two experimented ants was smaller for the ants walking not far from the nest (8 *versus* 10 correct responses). The two kinds of ants presented identical activity (0.950) with identical difference between the two observed ants ((1/10). There was nearly no difference between these two kinds of ants with regard to their caring of larvae which was of bad quality. Simply, those moving not far from the nest performed this task meanly probably 30 seconds sooner than the ants moving far from the nest.

Ants near the nest

These ants walked not very quickly and not very sinuously. The second observed ant walked somewhat but significantly more slowly than the first observed ant (χ^2 = 16.10, df = 1, P < 0.001), and with a significantly same sinuosity (χ^2 = 0.62, df = 1, 0.30 < P < 0.50). They rather well oriented themselves to the tied nestmate. The second observed ant oriented itself a little less well than the first observed one, but the difference was not significant (χ^2 = 0.76, df = 2, 0.50 < P < 0.70). They were not very audacious, and the first observed ant showed a higher value than the second ant, but this may be due to the fact that the sample was small: the difference was not significant (N = 5, T = 9.5, P = 0.359). They rather well perceived the rough character of the provided substrate, and the two observed ants differed with regard to this tactile perception. On the rough substrate, the first ant had a linear speed which was 0.9 mm/s less than the linear speed in its usual area (2.7-1.8) while the second ant had a linear speed which was 0.2 mm/sec less than that the linear sped in its usual area (2.1-1.9). In the same way, the first ant showed a sinuosity increase of 113 ang.deg./cm (383-270), while the second ant showed a sinuosity increase of only 55 ang.deg./cm (371-316). The change of locomotion was thus larger for the first ant which, consequently, better perceived the uncomfortable character of the substrate in comparison with the second ant. This difference of perception was in agreement with that relative to the perception of the alarm pheromone (see here above the results concerning the ants’ orientation to a tied nestmate).

The two experimented ants were identically aggressive towards the alien ant: they nearly continuously opened their mandibles and moved their gaster as if they aimed to sting this alien ant, though never stinging it. The difference between the number of times they presented the four considered levels of aggressiveness did not statically differ ($\chi^2 = 0.28$, df = 2, $0.58 < P < 0.90$), and the variable 'a' assessing their aggressiveness equaled 3.78 for one ant and 4.00 for the other ant. The first experimented ant hesitated several times to escape and finally escaped after 7 minutes; the second experimented ant also hesitated many times to escape and finally slowly escaped after 8 minutes. There is thus a little difference between the two ants. One of these ants gave 17 correct responses and the other one 13 correct responses during the 30 tests performed on them. The difference between the two ants was thus 4 correct responses and their mean conditioning score equaled 30/60 = 50%. These ants were rather active, with an activity equaling 0.700 for one ant and 0.900 for the other ant. Their mean activity equaled thus 0.800, and the difference between the activity of the two ants amounted 2/10. These ants were somewhat inclined to take care of the larva; one ant did so after 3 minutes, and the other ant after 2 minutes. The difference between the two observed ants equaled thus 1 minute and the mean time before performing the required task equaled 2 minutes 30 seconds.

Comparison of ants near the nest and ants not far from nest

These two kinds of ants largely differed. The ants staying near the nest walked far more slowly ($\chi^2 = 70.51$, df = 2, $P < 0.001$) and far more sinuously ($\chi^2 = 66.39$, df = 2, $P < 0.001$) than those moving not far from the nest. They even often stopped and did not walk. Also, unexpectedly, they less well oriented themselves towards a tied nestmate, even sometimes walking as if they simply ignored it, and this difference of orientation was statistically significant ($\chi^2 = 50.29$, df = 2, $P < 0.001$). Regarding their audacity, the value obtained for ants near the nest was inferior to that obtained for ants not far from the nest, but the difference was not significant, this being probably due to the fact that the sample was small (N = 8, T = -22.5, P = 0.296). Concerning the tactile perception, on a rough substrate, the ants not far the nest had a linear speed 19.5% lesser and an angular speed 59% higher than on a usual area, while the ants near the nest had a liner speed 23% lesser and an angular speed 35% higher. The linear speed of the two kinds of ants changed in the same way; their angular speed did not change similarly, but these events may be due to the already existing high sinuosity of the ants near the nest on a usual area. It can be concluded that the two kinds of ant equally perceived the uncomfortable nature of the substrate. The two kinds of ants differed with regard to their aggressiveness towards the alien ant; those staying near the nest being more aggressive than those moving not far from the nest. The difference between the number of times they presented the four considered levels of aggressiveness differed ($\chi^2 = 18.50$, df = 3, $P < 0.001$), and the variable assessing their aggressiveness equaled (mean values) 1.35 for ants not far from the nest and 3.89 for ants staying near the nest. No doubt that the latter have among their tasks the defense of the nest. There was a noticeable difference with regard to the ants' escaping ability or tendency to escape: the ants near the nest escaped slowly and hesitantly in 7' 30'' (mean value), while those moving not far from the nest escaped in 4 minutes. The ants staying near the nest reached a higher conditioning score than those moving not far from the nest (50.0% *versus* 43.3%), and the difference between the two experimented ants was smaller (4 *versus* 8 correct responses). The ants located near the nest were somewhat less active than those walking not far from the nest (0.800 *versus* 0.950), and the difference between the two observed was similar (1/10 *versus* 2/10). The ants present near the nest were more inclined to take care of a larva than those moving not far from the nest: they performed the task after 2 minutes 30 seconds (mean values) instead of after more than 3 minutes 30 seconds. The difference between the two experimented ants was smaller: 1 minute instead of 3 minutes.

Ants at nest entrance

The two experimented ants walked very slowly and sinuously. There was no difference between the two ants with regard to their linear speed

(χ^2 = 0.21, df = 1, 0.50 < P < 0.70) and a small difference with regard to their angular speed (χ^2 = 6.79, df = 2, P < 0.001). These ants did not well orient themselves towards a tied nestmate. They very poorly responded to the alarm pheromone emitted by the tied nestmate. In fact, the young ants do not know the significance of the alarm pheromone; they must learn it in the presence of older ants, progressively, in the course of their second or third year of life [6]. There was no difference at all between the poor orientation of the two experimented ants: this was obvious to observers and numerically as well as statistically verified (Table 1) (χ^2 = 0.23, df = 2, 0.80 < P < 0.90). The younger the ants were, the more similar they were; the older they were, the more different they became due to their experienced events. These ants presented a very poor audacity; they were not at all inclined to come onto the unknown apparatus. Their audacity, quantified based on the sighting of ants at a time on the apparatus, equaled 0.075 ants (the obtained mean value). The difference between the two experimented ants with regard to this behavior was not significant: N = 4, T = 10, P = 0.063. They soon returned at the nest entrance, simply looking to the apparatus. Obviously, each of the two experimented ants very well perceived the rough character of the provided substrate, walking on it at a very low liner speed (meanly: 1.4 mm/s) and a high sinuosity (meanly: 420 ang.deg./cm). The difference between each ant's linear and angular speed on the substrate and those on a normal area was χ^2 = 30.78, df = 1, P < 0.001 and χ^2 = 3.60, df = 2, 0.10 < P < 0.20, respectively for the first ant, and χ^2 = 52.52, df = 1, P < 0.001 and χ^2 = 16.02, df = 2, P ≤ 0.001, respectively for the second ant. Thus, with regard to their sensory perception, the difference between the two ants was small and only related to their sinuosity which was initially very high and had very less possibility to increase. The two experimented ants behaved in the same way in the presence of an alien ant: they often largely opened their mandibles, and frequently bended their gaster, but never stung the alien ants. There was no difference with regard to their presented levels of aggressiveness (χ^2 = 0.44, df = 1, P ≤ 0.50). The variable assessing the ants' aggressiveness level equaled 2.30 for the first ant and 2.36 for the second ant. The individual variability was thus very low between the two rather young experimented ants. Each of the two experimented ants did not escape before 9 minutes from the enclosure. They behaved exactly in the same way: they showed a delay in finding the exit, and when it was found, they hesitated, not knowing what to do, and continued to walk inside the enclosure until a time duration of 9 minutes, and finally went out of the enclosure slowly. One of the two experimented ants gave 20 and the other 16 correct responses over the 30 assessments made on each of them. The difference between them thus equaled 4 correct responses and their mean conditioning score amounted 36/60 = 60.0%. These ants were not very active: one ant had an activity of 0.550 and the other of 0.750. Their mean activity thus equaled 0.650, and the difference between them equaled 2/10. These ants were rather inclined to take care of a larva: one ant did so after 1 minute, the other ant after 1 minute 30 seconds. They thus performed the task after 1 minute 15 seconds (mean value), with a difference between them of 30 seconds.

Comparison of ants at nest entrance and ants near the nest

The ants at nest entrance walked more slowly and above all more sinuously than those located near the nest, and this was statistically significant (linear speed: χ^2 = 4.28, df = 1, 0.02 < P < 0.05; angular speed: χ^2 = 18.57, df = 1, P < 0.001). The ants staying at nest entrance permanently stayed there, moving very little. The ants located at the nest entrance oriented themselves less well than those moving near the nest; this was statistically verified (χ^2 = 6.62, df = 2, 0.02 < P < 0.05. The latter ants may have once or a few times perceived the alarm pheromone and learned how to respond to it, initiated to do so by older ants. Ants located at nest entrance may not yet have such an occasion, or only rarely. The ants staying at the nest entrance were far less audacious than those moving near the nest. Their behavior in front of the provided unknown apparatus very obviously differed: the ants at nest entrance stopped, walked away and rarely approached the apparatus, contrary to the ants moving near the nest. Let us recall that ants near the nest walking on a rough substrate presented a linear speed 23% less than that on a normal area and an angular speed 35%

greater than that on a normal area. For ants located at the nest entrance, these proportions equaled 21.13% and 9.44%, respectively. These lower proportions are only due to the fact that the ants located at nest entrance are already moving very slowly and sinuously on a normal area, and on the basis of observers' opinion, the ants at nest entrance perceived the rough character of the substrate as well as and may be better than those moving near the nest. Concerning their aggressiveness towards an alien ant, the two kinds of ants differed but not statistically. The variable assessing their aggressiveness level equaled 3.89 for the ants near the nest and 2.33 for those staying at the nest entrance: the former ants were thus more aggressive than the latter ones. However, there was no statistical difference with regard to the distribution of their aggressive levels: $\chi^2 = 2.42$, df = 1, $P \leq 0.30$. It could be concluded that the primary ants devoted to the colony defense are those moving near the nest (ants which are also devoted to be recruited if there are not enough ants moving not far and far from the nest), and that the secondary ants, constituting a reserve, devoted to the defense are those located at the nest entrance. The ants located at the entrance and those moving near the nest differed with regard to their escaping ability: the former escaped after 9 minutes while the latter did so after 7 minutes 30 seconds. The ants staying at the nest entrance reached a better conditioning score (60.0%) than those staying near the nest (50.0%). The difference between the two observed ants was identical: 4 correct responses. The ants staying at the nest entrance were less active than those moving near the nest (0.650 *versus* 0.800), and the difference between the two observed ants was identical for the two kinds of ant (2/10). The ants present at the nest entrance were more inclined to take care of the larva than those moving near the nest: they did so after 1 minute 15 seconds instead of after 2 minutes 30 seconds (mean values). The difference between the two observed ants was smaller: 30 seconds instead of 1 minute.

Ants in the entrance

These ants walked very slowly and very sinuously. They were not inclined to walk: being set out of the nest, in front of the entrance, they immediately tried to return inside the nest, having some difficulties in finding the entrance. There was no difference at all between the two experimented ants with regard to these behavioral and ethological traits (linear speed: $\chi^2 = 0.124$, df = 1, $0.70 < P < 0.80$; angular speed: $\chi^2 = 2.06$, df = 2, $0.30 < P < 0.50$). The two experimented ants did not orient themselves towards the tied nestmate. They seemed indecisive near it and very soon tried to re-enter the nest where they took their initial position in the entrance. This was obvious to observers and verified by the numerical results: the ants' orientation had a value nearly equaling 90 ang. deg. In addition, the two experimented ants did not differ with regard to this orientation behavior ($\chi^2 = 1.09$, df = 2, $0.50 < P < 0.70$). The two experimented ants did not come onto the unknown apparatus. In fact, only one of the two ants came on the edge of this apparatus for one second and immediately returned back on its way. The other ant never approached the apparatus. There was no statistical difference between the two ants with regard to this audacious behavior: N = 2, NS. On the basis of observations, the ants located in the nest entrance very well perceived the rough character of the provided artificial substrate: they walked there very slowly and very sinuously, (which was confirmed by the obtained numerical values). There was no statistical difference between the two experimented ants with regard to their speeds on a usual area. These was also no difference with regard to their speed on a rough substrate (linear speed: $\chi^2 = 0.83$, df = 1, $0.30 < P < 0.50$; angular speed ($\chi^2 = 1.34$, df = 2, $0.30 < P < 0.50$). The values of linear as well as of angular speed could thus be added for comparing those obtained for ants' walking on a usual and a rough area. It was found that the ants' linear speed was very less on a rough substrate than on a usual one ($\chi^2 = 127.64$, df = 1, $P < 0.001$), and that their angular speed was higher, though with a less level of probability ($\chi^2 = 8.38$, df = 2, $0.\ 30 < P < 0.50$). The observations were thus fully confirmed: the ants located in the nest entrance were very sensitive to the uncomfortable character of the provided substrate. Concerning their potential aggressiveness, the two experimented ants behaved similarly: they presented no aggressive behavior near the opponent alien ants; the variable assessing the aggressiveness equaled 0.048 for one ant and 0.054 for the other; their levels of aggressiveness were statistically similar (χ^2 = 1.002, df = 2, 0.50 < P < 0.70). The function of the ants located in the nest entrance was thus not at all the defense of the colony. The two experimented ants behaved identically while enclosed. They did not cautiously walk along the rim of the enclosure; they moved inside of it, and stayed for several minutes near the part of the rim facing the nest entrance, though the exit was farther. Finally, after 11 minutes, the ants slowly, hesitating, stopping, moving slowly again, walked through the exit and went out of the enclosure. There was no difference at all between the two ants which, as soon as out of the enclosure, returned inside the entrance exactly where they were before the experiment. These ants reached a rather high conditioning score over 12 hours: one ant gave 20 correct responses, the other 18 ones during the 30 assessments made on each of them. The difference between the two ants equaled 2 correct responses and their mean conditioning score was 38/60 (63.3%). These ants were not very active: one ant presented an activity of 0.650, the other ant 0.600. Their mean activity equaled thus 0.625, and the difference between the two ants was 0.5/10. These ants were inclined to take care of the provided larvae: one ant took a larva into its mandibles after 30 seconds; the other ant did so after about 20 seconds. They thus performed the task after about 25 seconds (mean value). The difference between the two experimented ants equaled 10 seconds.

Comparison of ants in the entrance (inside the tube) and ants at nest entrance (just at the opening of the tube)

The ants staying in the entrance walked more slowly and more sinuously than those located at the nest entrance (Figure 2). This was obvious to observers and was statistically confirmed (linear speed: χ^2 = 34.39, df = 1, P < 0.001; angular speed: χ^2 = 14.57, df = 2, P < 0.001). They may constitute a different class of individuals; the following comparisons are expected to check this presumption. The two kinds of ants differed with regard to their orientation towards a tied nestmate: those at nest entrance poorly oriented themselves, but those in the nest entrance did not at all orient themselves towards this stimulus. The former ants may have rarely and shortly perceived the species alarm pheromone and the alarm reaction of the workers, while the latter ants have very probably never experienced such an event, being thus unable to correctly respond to the alarm signal emitted by the tied nestmate. Statistically, the orientation behavior of the two kinds of ants differed (χ^2 = 16.75, df = 2, P < 0.001). The two kinds of ants slightly differed with regard to their audacious behavior in front of the unknown apparatus. Those located at the entrance came on this device 0.075 times while those located in the entrance came only 0.050 times (mean values), being thus not at all inclined to make dangerous, novel tasks. The difference between the two kinds of ants with regard to their audacity was not significant (N = 4, T = +4, -6, P = 0.433). The ants located in the entrance were more sensitive to the rough character of the artificial provided substrate than those staying at the nest entrance. Indeed, while the latter ants presented a decrease in linear speed of 21.13% and an increase in angular speed of 9.44%, the former ones presented a decrease in linear speed of 65.5% and an increase in angular speed of 13.3%. This was obvious to observers. The two kinds of ants largely differed with regard to their aggressiveness towards an alien ant. The variable assessing this aggressiveness equaled 2.33 for the ants staying at the nest entrance and 0.05 for those located in the nest entrance (mean values). Statistically, there was a high difference between the numbers of the five levels of aggressiveness presented by the two kinds of ants (χ^2 = 73.14, df = 2, P < 0.001). The ants at nest entrance were partly devoted to the colony defense, while those located in the entrance were not at all so. The two kinds of ants differed with regard to their 'ability' to escape from an enclosure. While those staying at the nest entrance looked for an exit after about 7-8 minutes and went out of the enclosure after 9 minutes, those located in the nest entrance did not do so during about 10 minutes and finally went out, hesitating, after 11 minutes. The ants located in the entrance reached a better conditioning score (63.3%) than those staying at the entrance (60.0%), and the difference between the two observed ants was smaller (2 *versus* 4 correct responses). The ants staying in the entrance were nearly as inactive as those staying at the nest entrance (0.625 *versus* 0.650), and the difference between the two observed ants was lower ((0.5/10 *versus* 2/10). The ants located in the nest entrance were more inclined than those staying at the entrance to take care of a larva: they did so after about 25 seconds instead of after 1 minute 15 seconds (mean values). The difference between the two observed ants was smaller: about 10 instead 30 seconds.

Ants inside the nest

These ants moved very slowly and sinuously, and there was no statistical difference with regard to this trait between the two experimented ants (linear speed: $\chi^2 = 0.22$, df = 1, 0.50 P < 0.70; angular speed: $\chi^2 = 1.83$, df = 1, 0.10 P < 0.20). They did not orient themselves towards a tied nestmate. On the contrary, they appeared to move away from it, to avoid it. There was no difference between the two experimented ants (with regard to this avoiding behavior ($\chi^2 = 0.049$, df = 1, 0.80 < P < 0.90). Their mean orientation value equaled 110.5 ang.deg. None of the two experimented ants were inclined to come onto the provided unknown apparatus. One ant came once on it, the other ant did not come. There was no difference between the two experimental ants: N = 1, NS. Over the 2 × 10 experimental minutes, they thus came 0.025 times (mean value). In fact, they avoided the apparatus and moved away from it. They were thus not inclined to make novel risky tasks. On the rough substrate, these ants walked somewhat more quicky than on a usual area ($\chi^2 = 86.75$, df = 1, P < 0.0.001). In fact, they tried to avoid the rough substrate, and stopped waking as soon as they were out of this substrate. On the rough substrate, they walked nevertheless more sinuously than on a usual area ($\chi^2 = 18.57$, df = 1, P < 0.0.001). The two experimented ants behaved exactly similarly during this experiment, with no difference at all with regard to their linear and angular speed ($\chi^2 = 2.21$, df = 2, 0.30 < P < 0.50 and $\chi^2 = 1.66$, df = 2, 0.30 < P < 0.50, respectively) and to their effort to come out of the rough substrate. In front of an alien ant, the two experimented ants behaved similarly ($\chi^2 = 0.102$, df = 1, 0.30 < P < 0.50). They never showed aggressive behavior towards the alien ant, did nothing or rarely made very short, not significant antennal contact, and at each encounter, went away from the opponent. Near the opponent ant, the experimented ants stayed with their head in a low position, oriented towards the ground, with their antennae folded orthogonally; they stayed motionless and did not touch the alien ant. The variable evaluating their aggressiveness equaled 0/43 for one ant and 0/40 for the other ant. Each two enclosed ants behaved similarly inside the enclosure. They moved without looking at a possible exit, or stayed motionless, even very near the exit without going to it and, through it, going out of the enclosure. After 12 minutes, none of the two experimented ants could escape. This observation was in agreement with that on these ants' audacity (see here above). These ants reached a high conditioning score. One of them gave 22, the other 21 correct responses over the 30 assessments made on each of them. The difference between the two ants equaled thus 1 correct response, and their mean conditioning score was 43/60 (71.6%). These ants were rather active, with an activity of 0.900 for one ant and of 0.750 for the other ant. Their mean activity was thus 0.825, and the difference between the two ants was 1.5/10. These ants were very inclined to take care of the provided larvae: they did so after 20 seconds with no difference between them.

Comparison of ants inside the nest and those in the entrance

The ants in the nest moved a little more quickly and sinuously than those staying in the entrance. In fact, the former ants moved, changed their location, relocated larvae, and cared the queens, while the latter ones did not move, stayed at their location doing nothing, apparently waiting for helping congeners when required. The linear speed of the former ants equaled 2.0 mm/s and their angular speed was 490 ang.deg./cm (man values), while these traits equaled 1.45 mm/s and 406 ang.deg./cm (mean values) for the latter ants (i.e., those staying in the nest entrance). Statistically, the two speeds differed between the two kinds of ants (linear speed: $\chi^2 = 23.63$, df = 1, P < 0.001; angular speed: $\chi^2 = 8.75$, df = 1, 0.001 < P < 0.01). The two kinds of ants also differed with regard to their orientation to a tied nestmate. This was significant ($\chi^2 = 13.03$, df = 1, P < 0.001). The ants moving in the nest avoided the tied nestmate more than the ants staying in the nest entrance. All occurred as if the former ants did not at all know the alarm pheromone, had never perceived it, while the latter ants had some notion of this pheromone, had sometimes perceived it, but still ignored the alarm reaction. Concerning their audacity, 0.025 ants moving inside the nest came onto the provided unknown apparatus while 0.05 ants staying in the nest entrance did so (mean values). The difference between the two experimented ants with regard to this audacious behavior was however not significant, the sample being too small: N = 3, NS. Taking into account of only the ants' angular speed on a usual and on a rough substrate, it appeared that their increase in sinuosity of movement equaled 10.20%, while that of ants staying in the nest entrance equaled 13.3%. The two kinds of ants were thus similarly sensitive to the rough character of the substrate. The ants moving inside the nest tried to avoid and to go out of the rough substrate more than those staying in the entrance, which explained the difference in their increased sinuosity proportions, and may indicate somewhat better sensitivity for the ants moving in the nest, which were probably younger than those staying in the entrance. There was some difference between the two kinds of ants with regard to their aggressiveness towards an alien ant. The variable assessing their aggressiveness equaled 0.05 for ants staying in the entrance and 0.00 for those moving inside the nest, near the brood. Statistically, the difference between the two kinds of ants with regard to their aggressiveness was significant ($\chi^2 = 14.86$, df = 2, $P < 0.001$). Concerning the escaping ability, there was some difference between the ants moving in the nest and those staying in the nest entrance: the former never escaped during the 12 experimental minutes, while the two experimented ants staying in the entrance could escape during this time period. The ants moving in the nest reached a higher conditioning score (71.6%) than those moving in the entrance (63.3%). Also, the difference between the two observed ants was smaller (1 *versus* 2 correct responses). The ants present inside the nest were more active than those present in the nest entrance (0.825 *versus* 0.625). Consequently, the difference between the two observed ants was larger (1.5/10 *versus* 0.5/10). The ants moving in the nest were more inclined to take care of the provided larvae than those present in the nest entrance: they performed the task after 20 instead of 25 seconds. The difference between the two observed ants was smaller: 0 instead of 10 seconds.

All these results which are described above are briefly illustrated in Figure 3, and numerically given in Table 1. They are also otherwise presented in Figure 4, the description of which is given in the conclusion section.

DISCUSSION

The results of all the experiments were in agreement with one another, for the ten considered traits as well as for the differences between the six kinds of ants, on the basis of the obtained numerical (for traits non statistically analyzed) and statistical results. They were also in agreement with what is generally reported in the documents (reviews, research articles, books) relative to the ant colony organization (to the references given in the Introduction section, let us add the work of Richardson and co-authors [17]). The findings of this study are more precise than those reported in the documents, defining at an ethological and physiological level the characteristics of different kinds of ants, and consequently the social organization of a colony. The social organization presented herein is valid for a brief time period, for one colony of a given species. During other time periods, as well as for other colonies and other ant species, the structure and the organization very probably differ. Among others, the organization may differ in the presence of sexual individuals, in the absence of a queen, and in species having workers devoted to honey reserve.

Every colony or social group of animals has its own kind of organization and structure. Each time, this gives them the most efficient functioning of their colony, the best efficacity for collecting food, taking care of the young individuals, building some nest, and defending the social group. This exists for e.g., in termites, wasps, bumblebees, bees, Cervidae, apes, and birds, and is highly, maximally developed in human societies. Studying such animal societies may provide not yet known information about processes which help to increase the advantages of a best possible social organization.

The difference between the two observed ants of each kind of ants was small, and even null, for those always present inside the nest, that is the young workers, but was rather large for those essentially moving far from the nest, that is the old workers. In fact, the difference increased from the former to the latter kinds of ants. Some idiosyncrasy exists thus in the examined colony, but essentially for the rather old ants, the very young being perhaps not very different from one another. Over their life and their experienced events, the ants progressively differ from each other, and idiosyncrasy develops. Each individual may not reach the oldest kind of workers, which forage far from the nest. Some idiosyncrasy may thus result from the kind of ant each individual reaches, e.g., moving not far from the nest though having the physiological characteristics of the ants moving far from the nest, staying at nest entrance though having the physiological characteristics of the ants located near the nest etc. Idiosyncrasy in ants has been reported in several experimental and theoretical works, e.g. [18].

When the amount of ants of one kind is to low, social regulation operates. It has been shown that this regulation often consists in a shift of younger ants performing the tasks of older ants, but can also consist in an inverse shift, i.e., that of older ants performing the tasks of younger ones [19]. This is true for each social group, including the human ones at any level (family, manufacture, country etc.).

In any way, social life is widespread, and gives rise to plenty interesting, useful, and applicable research topics.

CONCLUSION

Six different kinds of workers could be defined in a colony of the ant *M. sabuleti*, on the basis of ten of their ethological and physiological traits (Figure 3). Another figure (Figure 4) was elaborated using two traits for each graph. This representation clearly visualized the six kinds of ants considered.

The ants moving far from the nest

They walked quickly, well oriented themselves to a tied nestmate, were audacious, had a poor tactile perception, were not aggressive, could escape from an enclosure, did not soon acquire conditioning, were very active, and did not soon take care of a larva.

The ants moving not far from the nest

They walked rather quickly, well oriented themselves to a tied nestmate, were somewhat audacious, had a poor tactile perception, were not aggressive, could escape from an enclosure, did not soon acquire conditioning, were very active, and did not soon take care of a larva.

The ants moving near the nest

They did not walk quickly, poorly oriented themselves to a tied nestmate, were poorly audacious, had a poor tactile perception, were aggressive, could escape with delay from an enclosure, did not soon acquire conditioning, were rather active, and took care of a larva with delay.

The ants staying at the nest entrance

They did not walk quickly, not very well oriented themselves to a tied nestmate, were poorly audacious, had a good tactile perception, were aggressive, could escape with delay from an enclosure, acquired conditioning, were not very active, and took care of a larva with short delay.

The ants located in the entrance

They walked sinuously, did not orient themselves to a tied nestmate, were not audacious, had a good tactile perception, were not aggressive, could not escape from an enclosure, acquired conditioning, were not active, and quickly took care of a larva.

The ants moving inside the nest

They walked sinuously, did not orient themselves to a tied nestmate even moving away from it, were not audacious, had an excellent tactile perception, were not aggressive, could not escape from an enclosure, soon acquired conditioning, were rather active, and quickly took care of a larva.

Figure 4 shows that the six kinds of ants considered poorly overlapped themselves, and that some idiosyncrasy emerged in the colony between rather old ants (i.e., with regard to their aggressiveness when staying at the nest entrance).

This is valid for a time period, and for a given colony of *M. sabuleti*; it may vary over the seasons, may be subject to some social regulation, and differ from one colony to another. The difference between two ants of the same kind is null for those staying inside the nest; it is large for those moving far from the nest what leads to the occurrence of some idiosyncrasy.

CONFLICT OF INTEREST STATEMENT

The author affirms that there is no conflict of interest concerning this study.

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