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Cognitive differences between conspecific ant colonies

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Abstract

On the basis of previous observations, we presumed that cognitive differences exist between colonies of the same species. We assessed 10 ethological traits in four colonies of *Myrmica ruginodis* collected the same day from the same site and identically maintained in the laboratory. These traits were the ants' orientation to an alarm signal, trail-following behavior, crossing a path with twists and turns, escaping from an enclosure, acquiring and retaining visual conditioning, navigating a maze, replacing larvae in the nest in the absence or presence of a barrier, selecting a smooth path, establishing a single way, and pushing a door to reach a supply of sugar water. Each time, one of the colonies had the best score, another one was the least capable one, and the two others had intermediate capabilities, one of the latter being always slightly more able than the other. Such differences may exist for any social groups. Such collective behavioral differences between groups of the same species are likely to modify positively or negatively the fitness index of these groups and ultimately influence the species' evolution, even if the differences are based only on ethological traits.

INTRODUCTION

In the course of our studies on ants, we progressively became conscious that differences exist between similar colonies of the same species regarding their workers' abilities. After completing studies on most of these abilities, the ontogenesis of some of them [1, 2, 3, 4], and their range [5], we started analyzing the cognitive differences that may exist between similar colonies of the same species. We collected four demographically similar (queens, broods, workers) colonies of *Myrmica ruginodis* Nylander, 1846 on the same day at the same site, maintained them identically in the laboratory, and subjected them to ten experimental situations requiring cognition. The present paper describes this work. In the present section, we relate what is already known on the subject, summarize what we know about *M. ruginodis*, and cite the cognitive traits we intend to examine.

Having personally observed behavioral differences between colonies all along our studies on ants (a fact revealed in [6] and later on observed more conspicuously [5]), we were not very surprised when reading the work of Blight and co-authors [7]. These authors experimented on captive colonies of the ant *Aphaenogaster senilis* and demonstrated that these similar colonies exhibited different behavioral types and had different personalities. Idiosyncrasies are known to exist between individuals of the same species, a fact that has been reported in *Diacamma* ants [8] and that we have often observed in other ants [personal observations]. Since the members of an ant colony act together so that the colony becomes a "supra organism", it is plausible that some idiosyncrasies may also exist between colonies of the same species. Indeed, in social insects (as in any social animals), individual traits, including cognitive abilities, lead to collective performance of tasks, including those requiring cognition. The two levels, individual and collective, are linked, as illustrated by Dornhaus and Franks [9]. Consequently, in social insects, individual differences (= idiosyncrasies) may lead to differences at a higher, social level, a process explained by Jeanson and Weidenmüller [10]. The fact that societies of social insects can differ due to individual differences has already been noted by researchers and reviewed by Jandt et al. [11]. Additionally, in dogs, horses, monkeys, and birds, differences are commonly known to exist between different social groups of the same species [12]. To return to ants, the collection of four colonies of a well-known species (*M. ruginodis*) from the same site, at the same time, and in a similar demographic state gave us the opportunity to experimentally investigate potential cognitive differences between colonies of a given species. We know the species *M. ruginodis* rather well, having studied its eye morphology, subtended angle of vision, visual perception, navigation system, visual and olfactory conditioning, and recruitment strategy [1] as well as its spatiotemporal learning capability [13], expectative behavior [14], and ability in solving simple problems [5].

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In the present work, we examined the quality of response, i.e., the score or efficiency of the four collected colonies in the ten following ethological traits: orientation towards an alarm signal (i.e., a source of the species' alarm pheromone), trail-following behavior, cognition (i.e., traversing a path with twists and turns), escaping from an enclosure, visual conditioning ability and memory, navigating a maze with four choice points, replacing larvae in the nest in the absence or presence of a barrier, selecting a smooth path instead of a rough one, establishing a single way to facilitate the flow of traffic, and pushing a door to reach a supply of sugar water. The aim is not the study of the ants' behavior while presenting each of these ten traits, but the examination of potential differences between colonies as for their efficiency while presenting these traits. These potential differences between colonies result from differences between their workers' reactions. The assessments were thus made on individuals, groups, or entire colonies according to the examined traits.

MATERIALS AND METHODS

Collection and maintenance of ants

The experiments were conducted on four colonies of *M. ruginodis* collected on the same day at the same field site in the Aise Valley (Ardenne, Belgium) at the beginning of June 2016. The ants nested under stones. The colonies were demographically similar; they contained 500 - 800 workers, 1 - 2 queens and brood. They were exposed to identical luminosity, temperature, visual and olfactory cues, and food supply. They were maintained in the same way in the laboratory, in artificial nests made of 2 - 3 glass tubes half filled with water, with a cotton plug separating the ants from the water. New nest tubes were provided as necessary so that each colony relocated at its convenience. The inhabited nest tubes never dried or moistened. The nest tubes of each colony were deposited in a tray (34 cm x 23 cm x 4 cm), the internal sides of which were slightly covered with talc to prevent the ants from escaping. The trays served as foraging areas, and food was delivered in them similarly for the four colonies, i.e., at similar places and at the same time. The food consisted of an aqueous solution of sugar (30%) provided *ad libitum* in a small glass tube (diameter: 1.5 cm, length: 7 cm) plugged with cotton and of pieces of *Tenebrio molitor* larvae (Linnaeus, 1758) provided as meat three times a week on a glass slide. The ants were not starved when experimented. However, one day before the last experiment, they were deprived of their sugar water but not of their meat. The colonies were subjected to experiment from the beginning of June, after the emergences occurring in spring, until the beginning of September, before the emergences occurring in autumn. The colonies were thus demographically similar throughout the experimental work. The laboratory temperature was maintained at 18°C - 22°C, the relative humidity at approximately 80%. The lighting had an intensity of 330 lux while the ants were being tended or tested. At all other times, the lighting was provided by natural light through a window and varied from 5 to 120 lux according to the time of day. The ambient electromagnetic field had an intensity of 2-3 $\mu W/m^2$. Herein, the members of a colony are termed nestmates, as is commonly done for social Hymenoptera.

Experimental apparatus and methods

Orientation towards an alarm signal: The alarm pheromone of *M. ruginodis* is produced by the workers' mandibular glands, the attractive component being octanone. To examine the workers' orientation towards such a signal, the isolated head of a congener was deposited on a piece (1 cm^2) of strong white paper in the ants' foraging area (Figure 1A). The isolated head emitted the alarm pheromone just as an alarmed worker would. Its mandibles opened wide; the contraction of the abductor muscles led to the release of the contents of the mandibular gland reservoirs. To assess the ants' orientation towards the isolated head, the trajectories of 20 ants of each colony were recorded on a glass slide set above the colony's tray and later copied on transparent polyvinyl sheets using a water-proof marker pen. These transparent sheets could remain affixed to a PC monitor screen due to their own static electricity charge. The trajectories were then analyzed using specifically designed software [15]. Each trajectory was entered in the software by clicking on it every 5 mm with the mouse and then entering the location of the isolated head. Then, the total time of the trajectory was entered, and the software was asked to calculate the ant's orientation towards the isolated head. The orientation (O, here measured in angular degrees) is the sum of the angles, measured at each successive point of the recorded trajectory, made by each segment 'point i of the trajectory - head' and each segment 'point i - point i + 1', divided by the number of measured angles. If O was lower than 90°, the animal had a tendency to orient itself towards the head; if O was larger than 90°, the animal had a tendency to avoid the head. Each distribution of 20 values was characterized by its median and quartiles.

Trail-following behavior: The trail pheromone of *Myrmica* ants is produced by the workers' poison gland. Ten poison glands were isolated in 500 µl hexane and stored at -25°C. To perform one experiment, 50 µl of the solution was deposited, using a metallic normograph pen, on a circle (R = 5 cm) pencil drawn on a piece of white paper and divided into arcs of 10 angular degrees. One minute later, the piece of paper was set in the ants' foraging area. When an ant came into contact with the trail (Figure 1B), its response was assessed by the number of 10 angular degree arcs it walked without departing from the trail, even if it reversed its walking. If an ant turned back when coming in front of the trail, its response was assessed as "zero arc walked"; when it crossed the trail without following it, its response equaled "one arc walked". The trail-following behavior of 40 ants of each colony was assessed, and each distribution of 40 values was characterized by its median and quartiles.

Cognition, i.e., moving through twists and turns: This trait was assessed using an apparatus, one for each colony, described in [16], made of a small tray (15 cm x 7 cm x 4.5 cm) inside of which pieces of extra-strong white paper (Steinbach ®, 12 cm x 4.5 cm) were inserted in order to create a path with twists and turns between a loggia too narrow for 15 ants (the initial loggia) and a large one (Figure 1D). To conduct an experiment on a colony, 15 ants were set in the initial loggia. Then, the ants located in this initial loggia and in the large one were counted after 5 s and 2, 4, 6, 8, 10 and 12 min. The ability of the ants to cross the twists and turns is a direct function of the number of ants reaching the large loggia and an inverse function of the number of ants staying in the small loggia but is also a direct function of the rapidness with which the ants cross the twists and turns. Consequently, the ants' cognition was assessed by the variable 'sum of the 7 counts of ants in the large loggia / sum of the 7 counts of ants in the small loggia.

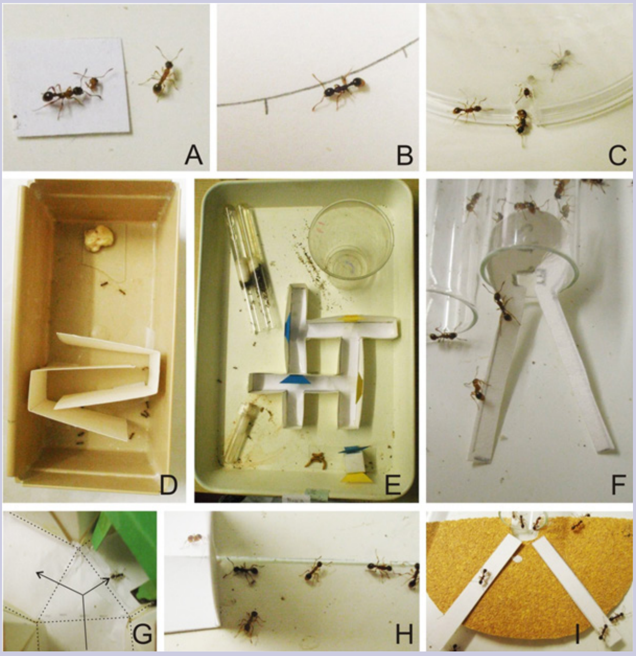

Figure 1. A: ants reacting to an isolated worker's head, a source of alarm pheromone. **B:** an ant following a circular trail. **C:** ants escaping from an enclosure through a notch in its rim. **D:** the apparatus used for assessing the ants' ability to traverse a path with twists and turns to leave a small zone. In the photo, two ants have reached the large zone. **E:** the experimental design used for studying the ants' navigation. The foraging area, the nest tubes, the sugar water, the maze with four choice points, the visual cues to the right and the left of the meat, and the cup where the tested ants were momentarily maintained are visible. **F:** the apparatus set in the nest entrance to induce ants to establish a single travel pattern for going in and out of their nest. **G:** an ant under visual operant conditioning giving the correct response when tested in a Y maze: it moves towards the branch containing the visual cue (a hollow green cube). The arrows indicate the two possible paths; the dotted lines mark the limits of the Y maze. **H:** ants in front of a glass barrier they must walk around in order to reach the nest entrance. **I:** the apparatus, made of a rough substrate and two smooth paths, set in front of the nest entrance, shows that ants primarily move on the smooth paths.

Escaping from an enclosure: For each colony, six ants were imprisoned in a reversed polyacetate glass (h = 8 cm, bottom diameter = 7 cm, ceiling diameter = 5 cm) set in the ants' foraging area. They were introduced into the glass through a hole (diameter = 3 mm) in the center of its ceiling. The lower part of the inner surface of the reversed glass had been slightly covered with talc to prevent the ants from climbing on it. The lower rim had been modified with a small notch (3 mm height, 2 mm broad), which allowed the ants escaping from the reversed glass (Figure 1C). The ants' ability to escape was quantified by counting the ants that had exited the reversed glass after 30 s, 1 min, 2 min, etc., up to 12 min. Table 1 gives the numbers of ants that had escaped after 6 and 12 min. The variable 'n° ants escaped after 12 min / 6' (6 being the initial number of captive ants) was also calculated for each colony.

Table 1. Differences between colonies in four ethological traits. Experimental details and statistics are given in the text. Briefly, each time, the colonies presented the same relative efficiency. For orientation and trail following, the median and quartile values are given.

Variables	colony A	colony B	colony C	colony D
1st time	39.5	64.0	60.2	58.6
Orientation towards an alarm signal (ang. deg.)	(35.6-47.6)	(43.3-82.8)	(47.0-74.7)	(43.5-64.3)
2nd time	39.5	65.4	62.4	57.9
	(34.3-50.8)	(50.6-84.6)	(48.7-69.7)	(37.4-66.1)
rank	*1*	*4*	*3*	*2*
Trail following: n° of arcs walked along the trail	12.5	5.0	8.0	9.0
	(8.0-19.0)	(3.0-10.5)	(5.0-11.3)	(6.0-16.0)
rank	*1*	*4*	*3*	*2*
Cognition: ants in the small (**s**) and the large (**l**) zone after	**s l**	**s l**	**s l**	**s l**
30"	12 0	13 0	13 0	12 0
2'	11 0	13 0	12 0	11 0
4'	9 0	10 0	10 0	9 0
6'	8 1	10 0	9 0	8 0
8'	7 2	9 0	8 0	7 0
10'	5 3	9 0	7 0	6 1
12'	4 4	9 0	7 1	7 2
Σ n° large zone/Σ n° small zone	0.170	0.000	0.015	0.050
rank	*1*	*4*	*3*	*2*
Escaping: n° of ants among 6, escaped after 6 and 12 min	6' 12' 3 5	6' 12' 2 1	6' 12' 2 3	6' 12' 3 4
final n° of ants escaped/6	0.83	0.17	0.50	0.67
rank	*1*	*4*	*3*	*2*

Visual operant conditioning capability and visual memory: At a given time, a hollow green cube under which ants could enter was set above the sugar water supply of each colony, subjecting the ants to visual operant conditioning. These cubes were made of strong paper as explained in [17]. The wavelengths reflected by the green paper had previously been determined. Tests were performed during training, when the ants were expected to acquire conditioning, and after removal of the green cube, when they were expected to partly lose their conditioning. Ants were individually tested in a Y-apparatus constructed of strong white paper and set in a tray (30 cm x 15 cm x 4 cm) as previously explained [17]. Each colony had its own Y-apparatus the sides of which were slightly covered with talc, and the floor was changed between the tests. The Y-apparatus was provided with a green hollow cube in one of its branches (Figure 1G). Half of the tests were conducted with the cube in the left branch, the other half with the cube in the right branch. Choosing the way with the green cube was considered the correct response. Control experiments were conducted before the ants were conditioned. To conduct a test on a colony, 20 ants were transferred one by one onto the area at the entrance of the Y-apparatus. Each ant was observed until it turned to the left or to the right, and its first choice was recorded when it was beyond a pencil-drawn line indicating the entrance of a branch (Figure 1G). Then, the ant was transferred into a polyacetate cup until 20 ants were tested; this prevented the same ant from being tested twice. All the tested ants were then returned to their foraging area. For each colony, the number of ants among 20 that gave the correct response was recorded, and the percentage of correct responses was established (Table 2).

Table 2. Differences between colonies in conditioning ability and memory. Experimental details and statistical results are given in the text. The four colonies acquired, and then retained, obviously different conditioning scores.

Time (hours)	Colony A	Colony B	Colony C	Colony D
Control	11/9 55%	10/10 50%	11/9 55%	10/10 50%
Conditioning				
7	14/6 70%	11/9 55%	12/8 60%	13/7 65%
24	15/5 75%	12/8 60%	13/7 65%	13/7 65%
31	15/5 75%	12/8 60%	13/7 65%	14/6 70%
48	16/4 80%	13/7 65%	14/6 70%	15/5 75%
55	17/3 85%	13/7 65%	14/6 70%	15/5 75%
72	17/3 85%	13/7 65%	14/6 70%	15/5 75%
rank	*1*	*4*	*3*	*2*
		(mean = 74%)		
Memory				
7	16/4 80%	11/9 55%	13/7 65%	14/6 70%
24	16/4 80%	11/9 55%	12/8 60%	14/6 70%
31	15/2 75%	10/10 50%	12/8 60%	13/7 65%
48	15/5 75%	10/10 50%	12/8 60%	14/6 70%
55	15/5 75%	10/10 50%	12/8 60%	13/7 65%
72	15/5 75%	10/10 50%	12/8 60%	14/6 70%
rank	*1*	*4*	*3*	*2*
		(mean = 64%)		

Navigation using learned visual cues: Ants of each colony were trained with an apparatus, shown in Figure 1E, made of a glass slide (2.6 cm x 7.6 cm) at one end of which a cube (2 cm x 2 cm x 2 cm) made of extra-strong white paper (Steinbach ®) was placed. On one face of the cube was a blue cue and on the opposite face a yellow cue. The cube was oriented so that the blue cue was on the left and the yellow cue on the right of the glass slide. Each cue was a piece of strong, colored paper (Canson ®) in the shape of a square (1.5 cm x 1.5 cm) and a trapezium (b = 1.5 cm; B = 3.5 cm) folded at 45°. Four pieces of *T. molitor* were deposited at the other end of the glass slide, 4 cm from the cube. In this way, the meat (= the reward) was 4 cm to the right of the blue visual cue and 4 cm to the left of the yellow visual cue. The pieces of *T. molitor* were renewed as necessary. After three and five days, ten ants from each colony were individually tested in a maze set in the ants' foraging area and adequately provided, at each choice point, with blue or yellow cues identical to those used for training. Two series of experiments (after 3 and 5 days) were performed to reveal any enhancement of the ants' navigation performance; the second experiment was not a simple pseudoreplication. Each maze was made of extra-strong white paper (Steinbach ®); the floor width and wall height equaled 2 cm, and the distance between two turns (points of choice for the ants) equaled 4 cm. The maze had no ceiling, its walls were slightly covered with talc, and a piece of white paper, renewed between the experiments, was placed on its bottom. For each experiment, ten ants from each colony were placed, one by one, in the maze, near the entrance. After an ant moved all along the maze, it was isolated in a polyacetate glass to avoid testing the same ant twice. For each choice point travelled by each tested ant of each colony, it was recorded whether the ant made an incorrect (= 0) or a correct (= 1) choice. This quantification yielded for each colony a total number of correct choices out of 10 for each choice point and out of 40 overall (4 choice points x 10 ants) (Table 3).

Table 3. Capabilities of four colonies in navigating. Tests were conducted in a maze with four choice points, after 48 h (1st score) and 72 h (2nd score) of training to two visual cues. Explanation and statistics are given in the text. The table gives the numbers of correct choices made by the ants. The four colonies differed as for their abilities in navigating the maze.

Colonies	**A**				**B**				**C**				**D**			
Choice points	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1st score (/10)	7	7	7	6	5	4	6	6	6	7	4	5	6	7	6	6
Total (/40)	27				21				22				25			
2nd score (10)	7	8	7	8	4	4	7	6	5	8	4	6	7	6	6	6
Total (40)	30				21				23				25			
rank	*1*				*4*				*3*				*2*			

Replacing larvae in the nest and walking round a barrier: Each colony had its own apparatus that formed a barrier on the ants' trajectories (Figure 1H). Two glass slides (7.5 cm x 2.5 cm x 1 mm) were inserted one above the other in two stands, each made of a piece of strong white paper (Steinbach®, 8 cm x 3 cm) folded orthogonally in order to present a vertical part (6 cm x 3 cm) and a horizontal one (2 cm x 3 cm) oriented towards the outside of the apparatus. The vertical parts were vertically pierced in the middle, from the bottom up to 5 cm height. The two glass slides were inserted one above the other in the two obtained slits.

In the first phase, more than 10 larvae and workers were removed from their nest in the absence of a barrier, and a first assessment was conducted. In the second phase, an apparatus was set 3 cm in front of the nest entrance, and more than 10 larvae and workers were removed from the nest and deposited in the area lying in front of the barrier on the side not facing the entrance. A second assessment was then conducted. In the third phase, a second experiment similar to the latter one was performed and a third assessment was made. This second experiment was not a simple pseudoreplication; its aim was to detect any learning of the behavior required in such circumstances. Each time, two traits were assessed in the course of two experiments: the time taken by the ants to replace the larvae in the nest and the ants' orientation towards their nest entrance.

To assess the time taken by the ants to replace the larvae, the time elapsed since the start of the experiment was noted when 1, 2, 3 … 10 larvae were replaced. The shorter these times were, the more capable the ants were at replacing their larvae in the nest and at walking round the barrier.

To assess the ants' orientation towards the nest entrance, the trajectories of 10 ants from each of the four colonies were recorded and analyzed as explained above (orientation towards an alarm signal) [15]. Theoretically, the ants' orientation towards their entrance would be less than 90° in the absence of a barrier and of lower quality in the presence of it, though not larger than 90° if the ants could walk round the barrier [5]. Either way, the lower the orientation value, the more effectively the ants would move in the direction of the entrance, either directly or around the barrier.

Selecting a smooth path instead of a rough one: An apparatus was constructed for each of the four colonies (Figure 1I). It consisted of a half circle of abrasive paper (emery n° 280, diameter = 4 cm), with a half-circular notch (diameter = 1.2 cm) in its center, and of two pieces of smooth, extra-strong white paper (Steinbach®, 0.5 cm x 4 cm) deposited on the abrasive paper, each one along a radius, the angle between the two radii equaling approximately 80°.

To perform an experiment on a colony, such an apparatus was set in front of the nest entrance, with the notch of the apparatus touching the entrance. Ants and larvae were then removed from the nest and deposited beyond the abrasive paper. The ants had to cross a space 3 cm long to enter and exit their nest, moving on the abrasive and/or the smooth substrate. The ants moving on each of the two substrates (rough = r and smooth = s) were counted each 30 sec for 10 min, and the numbers obtained during the first five and the last five minutes were separately added for each colony. One day later, the experiment was repeated. We considered this second experiment not to be a pseudoreplication. It was conducted to assess whether the ants learned the behavior required in the present circumstances. According to the surface area of the rough substrate lying between the two pieces of smooth paper (and allowing going in and out of the nest) and to the surface of the latter, if ants equally walked on the two types of substrate, approximately 2.5 times more ants would be seen on the rough substrate [5]. Consequently, s x 2.5 / r quantified the ants' preference for the smooth substrate.

Establishing a single way: An apparatus was constructed for each colony (Figure 1F). It consisted of a piece of extra-strong white paper (Steinbach®) made of a circular part (diameter: 1.1 cm) with a rectangular hole (4 mm x 2 mm) and of two linear parts (4 cm x 2 mm), one oriented to the left, the other to the right of the circular part of the apparatus. Each linear part was 2 mm wide, which was too narrow to accommodate two ants side by side.

To perform an experiment on a colony, approximately 10 ants and larvae were removed from the nest and deposited in front of it at a distance of approximately 6 cm. Then, the circular part of an apparatus was inserted in the nest entrance, which thus became limited to the small hole in the circular part of the apparatus now standing vertically. The two linear parts of the apparatus were lying on the foraging area in front of the entrance. Then, the ants moving on the left and the right linear parts of the apparatus and going towards or away from the nest entrance were counted each 30 sec for 10 min. The numbers obtained during the first five and the last five minutes were separately added for each colony. A variable was set up for assessing the ants' establishment of a single way: n° ants moving 'in' on the left path/ n° ants moving 'out' on the left path X n° ants moving 'out' on the right path/ n° ants moving 'in' on the right path.

Pushing a polyvinyl door to reach a sugar water supply: One apparatus was built for each of the four colonies. It consisted of a tube, of the type used for providing sugar water to the ants, closed off with transparent polyvinyl. To do so, a piece of polyvinyl made of an upper rectangular part (2.5 cm x 1 cm) and a lower circular one (diameter = 1.5 cm) was used. Using Sellotape®, the upper part of the piece was attached to the tube containing sugar water, above the entrance of the tube. Consequently, the lower part of the polyvinyl piece hung just in front of the entrance, which became entirely though weakly blocked. The ants could recognize their usual feeder and probably perceive the sugar water. However, they could not simply walk up to the sugar water: they had to push the lower circular part of the polyvinyl piece (i.e., the door) to reach the impregnated cotton that plugged the part of the tube filled with sugar water.

To conduct the experiment, the usual tubes containing sugar water were removed from the ants' foraging area (this was the only time the ants were partly deprived of food), and one day later, at t = 0, at a time when the ants wanted to drink, an experimental apparatus was set in each foraging area at the place where the sugar water supply was previously. Since that time, the number of ants drinking the sugar water after having pushed the door was recorded every 5 min for one hour for each colony, and the mean value of the 12 counts was established in each case.

Statistical setup and analysis: We avoided repeating experiments and conducting pseudoreplications, which should have reduced the level of probability. Each time we conducted a second similar experiment, we were in fact assessing a novel trait (i.e., the learning of the best behavior to exhibit). There was an exception: we repeated our first experiment (the assessment of the ants' orientation), having been rather surprised by the results, and we found identical results. The data were recorded by an observer who was looking at the ants and thus was not blind to the situation. Thereafter, the variables were assessed and the data analyzed by an investigator blind to the situation, using a calculator and adequate software. In order to have four colonies in the same demographical state, we had to experiment after the emergences occurring in spring and before those occurring in autumn. We had 3 months to examine 10 traits in 4 colonies. We thus used samples of medium size (10, 15, 20 individuals) and not very large ones (50 to 60 individuals, which would have imperiled the timing). We thus used non-parametric tests [18], as is commonly done in ethology. The non-parametric χ^2 test was used for comparing colonies with respect to the ants' orientation to an alarm signal, trail-following behavior, and orientation to the nest entrance in the absence or the presence of a barrier. The non-parametric χ^2 test for 2 x 2 contingency tables was used for studying the ants' use of smooth paths and their propensity to push a door. The non-parametric χ^2 goodness of fit test allowed us to study the ants' establishment of a single way. The non-parametric Wilcoxon test was used for evaluating the difference of ants' cognition, conditioning ability and memory, navigation, and time taken to replace larvae in the nest in the absence or the presence of a barrier. These well-known tests were appropriate for revealing differences between the colonies.

RESULTS

Orientation towards an alarm signal

The results of the first and second experiments were in agreement (Table 1, orientation, 1st time, 2nd time), the latter experiment being a pseudoreplication. Each time, workers of colony A oriented themselves very well towards a source of alarm pheromone (orientation median value = 39.5°; Figure 1A), those of colony B did so badly (median value ~ 65°), and those of colonies C and D oriented themselves slightly better than those of colony B (median value ~ 61° and 58° for colonies C and D, respectively). For the first experiment, the difference of orientation between colonies A and B was significant ($\chi^2 = 6.54$, df = 2, $P \sim 0.01$), that between colonies A and C was at the limit of significance ($\chi^2 = 3.95$, df = 1, $P \sim 0.05$) and that between colonies A and D was not significant ($\chi^2 = 4.26$, df = 2, $0.10 < P < 0.20$). For the second experiment, these differences were at the limit of significance between colony A and B ($\chi^2 = 3.75$, df = 1, $P \sim 0.05$), not significant between colonies A and C ($\chi^2 = 2.67$, df = 1, $0.10 < P < 0.20$) and not at all significant between colonies A and D ($\chi^2 = 0.79$, df = 1, $0.30 < P < 0.50$). Thus, based on the observations, the obtained numerical values and the statistical results, it could be stated that colony A perfectly responded to an alarm signal, colony B did so poorly, and colonies C and D did so with an intermediate efficiency, colony D responding better than colony C. The mean of the four median values here obtained (55.9 ang. deg) was in the range of the median value obtained in 1989 in a study on the response of *M. ruginodis* workers to their mandibular glands (49.5 ang. deg., [unpublished data of 19]).

Trail-following behavior

Numerical results are presented in Table 1, trail following. Ants of colony A perfectly followed the presented circular trail (Figure 1B), but those of colony B did so poorly. The difference of trail-following capability between these two colonies was highly significant ($\chi^2 = 20.695$, df = 2, $P < 0.001$). The trail following of colonies C and D was intermediate, and their following scores significantly differed ($\chi^2 = 15.31$, df = 2, $P < 0.001$). In contrast, the difference between colonies A and D was not significant ($\chi^2 = 2.59$, df = 2, $0.20 < 0.30$). On the basis of the obtained values and of the statistical results, it could be stated that colony A was the most efficient in following a trail, colony D was slightly less efficient, colony C was less efficient, and colony D was the least efficient. The mean value of the four median values here obtained (8.6 arcs of 10°) was in the range of that obtained in a previous study (1989) on the response of *M. ruginodis* workers to their poison gland extract (6.9 arcs of 10°, [unpublished data of 19]).

Cognition, i.e., ability to move through twists and turns

Results are given in Table 1, cognition. Workers of colony A efficiently moved through the twists and turns (Figure 1D). After the 12 experimental minutes, four ants had reached the large loggia, beyond the twists and turns. Ants of colonies C and D also entered the twists and turns, but in the 12 experimental minutes, only one ant for colony C and 2 for colony D reached the large loggia. No ant of colony B reached the large loggia. Based on the numbers of ants remaining in the small loggia, the difference of ants' cognition was significant between colonies A and B (N = 7, T = 28, P = 0.008), significant between colonies A and C (N = 7, T = 28, P = 0.008), at the limit of significance between colonies B and C (N = 4, T = 10, P = 0.063), not significant between colonies A and D (N = 2, no T value), and significant between colonies C and D (N = 6, T = +4, -2, no P value). The difference was thus significant only between colony A and colonies B or C. The variable assessing the ants' cognition clearly revealed the relative ability of each colony, which could be ranked in the same order as in the two previous experiments.

Escaping from an enclosure

Numerical results are given in Table 1 (escaping), and a photograph of captive ants escaping is given in Figure 1C. Workers of colony A soon found the hole provided in the rim of the enclosure and escaped. Only one ant among six was still captive after the 12 experimental minutes. The variable assessing the ants' ability in escaping equaled 5/6 = 0.83. Workers of colony B moved over the entire area lying under the reversed glass and not systematically along the rim. Only one ant among six escaped; the variable assessing the ants' ability in escaping equaled 1/6 = 0.17. Ants of colonies C and D moved all around but also along the rim; 3 ants for colony C and 4 for colony D escaped, the variables assessing their ability equaling 3/6 = 0.50 and 4/6 = 0.67, respectively. Once more, even if at first sight the ants of each colony appeared to behave similarly, colony A was the most expert in finding the exit of the enclosure, colony B was the least, and colonies C and D had intermediate abilities, colony D being somewhat more able than colony C. The four colonies could thus be ranked in the same order as for the three previous experiments.

Visual conditioning ability and visual memory

The numerical results are given in Table 2, and a photo of a tested ant is shown in Figure 1G. Before being trained, ants of each colony went randomly to the right and to the left branch of the Y maze. Under training, ants of colony A very quickly acquired visual conditioning. After only 7 hours of training, they reached a score of 70% of correct responses, and they reached the final score of 85% after only 55 hours. In contrast, ants of colony B reached the poor final score of 65% after 48 hours of training. The difference of conditioning ability between the two colonies was significant (N = 6, T = 21, P = 0.016). Ants of colonies C and D acquired visual conditioning more slowly than those of colony A, but more rapidly than those of colony B, and reached final conditioning scores of 70% and 75%, respectively. The difference between their respective abilities was slightly significant (N = 5, T = 15, P = 0.031). The difference between colony A and colony C or D was significant (N = 6, T = 21, P = 0.016). The difference between colony B and colony C or D was also significant (N = 6, T = 21, P = 0.016). In conclusion, concerning their ability in acquiring visual conditioning, colony A was the most able, colony D was a little less able, colony C was still a little less able, and colony B was the least one.

After removal of the visual cue, the ants of colony A kept a conditioning score of 75% even after 72 hours, ants of colony B lost their learning in a few hours, and ants of colony C and D retained 60% and 70% of their learning, respectively. The difference between colony A and colony B, C, or D was significant in each case (N = 6, T = 21, P = 0.016). Colony A thus showed the strongest memory. The difference between colony B and colony C or D was significant (N = 6, T = 21, P = 0.016). Colony B thus presented the weakest memory. The difference between colonies C and D was significant (N = 6, T = 21, P = 0.016): colony D had a slightly stronger memory than C. The ranking for memory was thus the same as that for conditioning.

The mean values, for the four colonies, of the acquired conditioning score and the retained one equaled 74% and 64%, respectively, i.e., the values previously found when the visual conditioning of *M. ruginodis* was studied for the first time [17].

Navigation performance

Numerical results are given in Table 3. Ants of colony A quickly learned to use the two learned visual cues to navigate the maze efficiently: they reached scores of 27/40 and 30/40 after 48 and 72 hours, respectively. Ants of colony B reached the very low score of 21/40 after 48 hours and remained at the same score after 72 hours. This was in agreement with the fact that colony B had visual conditioning of poor quality. Ants of colonies C and D reached intermediate scores after identical time periods: 22/40 and 23/40 for colony C and twice 25/40 for colony D after 48 and 72 hours, respectively. The difference between colony A and colony B at t = 72 hours for the scores obtained at each choice point was at the limit of significance (N = 4, T = 10, P = 0.063). The differences between all the other pairs of colonies (A-C, A-D, C-D, B-C, B-D) were not significant (N = 3, T = 6 or 5, P = 0.125 or 0.250, NS). Consequently, colony A was the most efficient in navigating, colony B was the least efficient, and colonies C and D had intermediate efficiencies, colony D being slightly more efficient than colony C.

Replacing larvae in the nest and walking around a barrier

It was previously demonstrated that *M. ruginodis* workers replaced in the nest larvae experimentally removed from it (an ant's usual behavior) and that they could do so by walking around a barrier. Differences appeared between colonies as for their efficiency in doing so (Table 4, Figure 1H). In the absence of a barrier in front of their nest entrance, ants of colony A soon replaced 10 larvae removed from the nest (in 240 sec = 4 min) and oriented themselves well towards the entrance (orientation = 66.9 ang. deg). Ants of colony B did so more slowly (in 600 sec = 10 min) with a poor orientation (80.6 ang. deg.). The difference between the two colonies was significant: time: N = 10, T = 55, P = 0.001; orientation: χ^2 = 3.81, df = 1, P ~ 0.05. Ants of colonies C and D behaved less effectively than those of colony A but more effectively than those of colony B, and ants of colony D performed somewhat better than those of colony C (time: 390 sec vs 450 sec = 6.5 min vs 7.5 min; orientation: 72.5 ang. deg. vs 75.0 ang. deg., respectively). Colonies A and C statistically differed only in the time taken to replace the larvae in the nest (time: N = 8, T = 36, P = 0.004; orientation: χ^2 = 1.25, df = 1, 0.20 < P < 0.30); colonies A and D also statistically differed only in that variable (time: N = 9, T = 45, P = 0.002; orientation: χ^2 = 0.39, df = 1, 0.50 < P < 0.70). Colonies C and D only slightly differed in time taken (time: N = 5, T = 15, P = 0.031; orientation: χ^2 = 0.33, df = 1, 0.50 < P < 0.70). Consequently, as for ability in replacing larvae into the nest, colony A was the most efficient, colony D was less efficient, colony C was even less efficient, and colony B was the least efficient.

Table 4. Comparison of four colonies' efficiency at replacing larvae in the nest, without or with a barrier in front of the nest entrance. Experimental details and statistics are given in the text. The colonies had different ability levels, as revealed by the time they spent in replacing 10 larvae and by their orientation (median and quartile values) towards the entrance.

Colonies	**Time (seconds) to retrieve**											**Orientation to the entrance (ang. deg.)**	
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10 larvae**			
	without barrier										*rank*		*rank*
A	30	60	70	80	90	105	120	150	180	240	*1*	66.9 (59.9 – 75.4)	*1*
B	60	105	120	240	300	360	420	480	540	600	*4*	80.6 (73.2 – 88.3)	*4*
C	30	60	90	120	150	180	270	330	390	450	*3*	75.0 (68.7 – 80.9)	*3*
D	45	60	90	120	150	180	210	270	330	390	*2*	72.5 (70.9 – 76.4)	*2*
	with a barrier										*rank*		*rank*
A	60	120	150	180	210	240	270	300	330	420	*1*	70.0 (66.8 – 77.5)	*1*
B	120	150	180	210	300	360	480	600	1200	1800	*4*	89.6 (81.8 – 95.2)	*4*
C	30	60	120	180	240	270	360	390	450	600	*3*	84.7 (79.1 – 86.1)	*3*
D	60	120	150	180	210	240	300	360	420	540	*2*	79.0 (73.7 – 82.9)	*2*
	with a barrier, second time										*rank*		*rank*
A	10	20	30	60	80	90	110	130	150	180	*1*	68.1 (65.8 – 73.7)	*1*
B	60	120	180	210	240	270	330	360	420	470	*4*	86.1 (79.6 – 91.6)	*4*
C	30	60	90	110	120	150	180	230	240	290	*3*	78.6 (76.4 – 87.8)	*3*
D	60	90	120	150	180	210	240	290	300	330	*2*	76.9 (65.8 – 83.7)	*2*

In the presence of a barrier placed for the first time, the time taken by the workers to replace ten larvae in the nest was less than twice the time spent without a barrier for colonies A, C and D, but equaled three times the time spent without a barrier for colony B. The difference between colonies A and D was at the limit of significance (N = 4, T = 10, P = 0.063), while that between colonies A and C was significant (N = 9, T = 39, P = 0.027). The ants' orientation towards the entrance was of course poorer than in the absence of a barrier, the differences equaling 3.1°, 9°, 9.7°, and 6.5° for colonies A, B, C, and D, respectively. The most efficient colony was thus colony A, and the least efficient was colony B (with the longest time spent). Colonies C and D had intermediate efficiencies, colony D being somewhat more efficient than colony C (+ 6.5° instead of +9.7°).

During the second experiment with a barrier, each four colonies performed better: the ants took less time to replace the larvae, and they oriented themselves better towards the entrance. Nevertheless, colony A was still the most efficient one, colony B the least efficient, the difference between the two colonies being statistically significant (time: N = 10, T = 55, P = 0.001; orientation: $\chi^2 = 7.20$, df = 1, $P < 0.001$). Colonies C and D had intermediate efficiencies, still differing from colony A as for the time taken to replace the larvae (time: colony C or D: N = 10, T = 55, P = 0.001; orientation: for colony C: $\chi^2 = 0.96$, df = 1, $0.30 < P < 0.50$; for colony D: $\chi^2 = 1.98$, df = 1, $0.10 < P < 0.20$).

Consequently, concerning the ants' ability in replacing larvae in the nest and in walking around a barrier, the four colonies in decreasing order of ability were A, D, C, and B.

Selecting a smooth path instead of a rough one

It was previously shown that *M. ruginodis* workers had a tendency to move on smooth paths instead of on a rough substrate. The four colonies presented differences in doing so (Table 5, Figure 1I). The variable assessing the ants' preferential use of the smooth paths revealed that this behavior increased in the course of the ten experimental minutes but did not improve after the first experiment. Comparing the values obtained for the variable assessing the ants' use of the smooth paths during the first and the second experiment revealed that colony A was the most expert in doing so, that colony D was a little less, that colony C was still less and that colony B was the least expert. Statistical analysis could not be conducted on this variable but could be conducted on the sum of the numbers of ants counted during the first and the second experiments, during the first and the last five minutes, on one hand on the rough substrate, and on the other hand on the smooth paths. This analysis revealed that colonies A and B significantly differed (A: 36 and 58 vs B: 71 and 49; $\chi^2 = 8.37$, df = 1, $P < 0.001$) and that colonies A and C also differed (A: 36 and 58 vs C: 95 and 66; $\chi^2 = 9.19$, df = 1, $P < 0.001$), but that colonies A and D did not (A: 36 and 58 vs D: 48 and 49; $\chi^2 = 1.99$, df = 1, $0.10 < P < 0.20$). Consequently, based on the observation, the variable assessing the ants' use of the smooth paths, and the statistical results, it can be stated that colony A obviously prioritized the smooth paths, colony D did so a little less effectively, colony C not as effectively, and colony B far less.

Table 5. Use by four colonies of a smooth substrate and a rough one, 2.5 times larger, for going in and out of the nest. Experimental details and statistical results are given in the text. Briefly, the ants of the four colonies progressively used the smooth paths to a different extent, as revealed by the values, given in the table, of a variable assessing such a choice.

Experiment	**Colonies**			
N° time	**A**	**B**	**C**	**D**
I 0' – 5'	20x2.5/17=2.94	12x2.5/21=1.45	20x2.5/36=1.40	11x2.5/18=1.53
rank	*1*	*4*	*3*	*2*
5' – 10'	13x2.5/2=16.25	13x2.5/14=2.32	17x2.5/17=2.50	13x2.5/9=3.61
rank	*1*	*4*	*3*	*2*
II 0' – 5'	15x2.5/13=2.88	11x2.5/20=1.38	15x2.5/27=1.39	12x2.5/13=2.31
rank	*1*	*4*	*3*	*2*
5' – 10'	10x2.5/4= 6.25	13x2.5/16=2.03	14x2.5/15=2.33	13x2.5/8=4.06
rank	*1*	*4*	*3*	*2*

Establishing a single way

It was previously demonstrated that *M. ruginodis* workers can establish a single way when they have only two narrow paths for entering and exiting their nest (Figure 1F). The ability of the four tested colonies to do so was compared herein (Table 6). The variable assessing the ants' establishment of a single way showed that colony A was the most able in doing so (variable = 17.0), colony B had poor ability (variable = 4.3), and colonies C and D presented intermediate capabilities, colony D being somewhat more able than colony C (variables = 7.2 and 5.5, respectively). Statistically, only colonies A and B differed: $\chi^2 = 3.18$, df = 1, $P \sim 0.05$. Consequently, the four colonies established a single way more or less accurately, colony A being the most able, colony D being a little less, colony C being still less, and colony B being the least able.

Table 6. Single way established by four colonies having only two very narrow paths for entering and exiting their nest. Each colony succeeded in establishing a single way but they did so with different efficiencies. Details can be found in the text.

Paths		**colony A**			**colony B**			**colony C**			**colony D**		
directions		0'–5'	5'–10'	**T**	0'–5'	5'–10'	**T**	0'–5'	5'–10'	**T**	0'–5'	5'–10'	**T**
Left	in	12	6	**18**	7	6	**13**	9	9	**18**	6	6	**12**
	out	3	3	**6**	5	0	**5**	4	2	**6**	3	3	**6**
Right	in	1	2	**3**	4	2	**6**	2	4	**6**	3	2	**5**
	out	9	8	**17**	6	4	**10**	7	4	**11**	8	10	**18**
'single way' variable		18/6x17/3=**17.0**			13/5x10/6=**4.3**			18/6x11/6=**5.5**			12/6x18/5=**7.2**		
rank		*1*			*4*			*3*			*2*		

Pushing a door to reach a sugar water supply

It was previously shown that the oldest ants can push a door (made of polyvinyl) to access their sugar water supply. The present work revealed that each colony differed as for their performance in doing so. The total number of ants that reached the sugar water beyond the door during the experimental time period equaled 15 for colony A, 3 for colony B, 8 for colony C and 14 for colony D. Colony A was thus the most able in accomplishing the task, colony D was similarly able, colony C was less able and colony D was the least able. Statistically, colonies A and B differed ($\chi^2 = 3.13$, df = 1, P ~ 0.05), colonies A and C did not ($\chi^2 = 0.56$, df = 1, $0.30 < P < 0.50$), colonies A and D of course did not differ (counted numbers = 15 and 14), and colonies C and D also did not differ ($\chi^2 = 0.37$, df = 1, $0.50 < P < 0.70$). The numerical results, the statistical analysis, and the observations enabled us to rank the colonies once more in the decreasing order A, D, C, and then B.

Supplementary observations

After the end of the ten related experiments, each colony similarly needed a new nest tube. They were thus provided with such nest tubes at the same time and given the opportunity to relocate. Colony A did so in 2-3 days, colonies C and D in 6 days, and colony B in 17 days. These differences in the relocation time between the colonies were in agreement with the differences observed in the course of the present work. Finally, the total time during which the four colonies always presented the same rank of cognitive ability equaled 17 weeks (3 ½ months), which corresponds to nearly 10 years for humans. Our observations thus lasted for an extended time period sufficient for the conclusion that effective differences exist between demographically similar colonies.

Later, we studied the effects of paroxetine, a largely used antidepressant, using two demographically similar colonies of *Myrmica sabuleti* Meinert 1861 collected at the same time from the same field. In the course of ten experiments dealing with the ants' cognitive abilities, the two colonies always ranked in the same order: the same colony was always the most efficient. This observation confirmed those made in the current study.

DISSCUSSION

For a long time, we have speculated that differences exist between similar colonies of the same ant species with respect to their cognitive performance and their ability in performing tasks. We thus undertook an appropriate ethological work to examine this presumption. We worked on four similar colonies of *M. ruginodis* from June to September. We discovered that these colonies responded in the same way but with different scores when submitted to 10 different tests. The four colonies could always be ranked in the same order as for their orientation to an alarm signal, trail-following behavior, cognition, ability in escaping from an enclosure, conditioning ability, memory, navigation, replacing larvae in the nest without or with a barrier in front of the entrance, selecting a smooth path instead of a rough one, establishing a single way when only two very narrow passages were available, and pushing a door to reach a supply of sugar water (Figure 2). After the end of the experiments, the colonies were allowed to relocate. They did so more or less rapidly, i.e., in different time periods in agreement with the level of their cognitive abilities revealed herein. The total time during which the colonies permanently ranked in a given order as for their cognitive abilities equaled 17 weeks, a time period corresponding to 10 years for a human being. After collecting the data (trajectories, numbers of ants, numbers of responses, etc.) without being blind to the colony identities, we analyzed these data with software and/or a mini-calculator while being blind to the situation. The ethological differences observed between colonies, even if always in agreement with one another, were perfectly valid.

Figure 2. Schematic representation of the efficiency or the score presented, in the course of the assessment of 10 traits (column 1), by four colonies (A, B, C, D) of *Myrmica ruginodis* that were demographically similar and that lived in the wild on the same site. Numerical details are given in Tables 1 to 6, and the measurement of each trait is explained in the text. Briefly, colony A was always the highest performer, colony B the lowest, and colonies C and D intermediate, with colony D always modestly outperforming colony C.

These differences might be explained by slight genetic, morphological, and/or physiological differences existing between the workers of the different colonies. We know, for instance, that there exists a large amount of variation in the eye morphology and the number of ommatidia of the workers, this variation nonetheless being lower than that existing between species [1]. Similar differences might exist for the sensory cells of the antennae. The visual and olfactory perception of the individuals belonging to different colonies may thus differ. This may impact their orientation to an alarm signal, trail-following behavior, conditioning (association between cues and rewards) and memory, navigation, and orientation to the nest entrance. The differences observed between colonies may also be due to the life circumstances experienced by the individuals: the presence of many cues requiring memorization, nest relocations increasing the individuals' ability in navigation and transporting larvae, or encounters with large prey and/or enemies reinforcing the individuals' cooperation. Such experiences may account for the observed differences in cognition, escaping from an enclosure, walking around a barrier, selecting the best paths, establishing a single way, and pushing a door.

Differences of the same type as those here reported may have been encountered by Reichle [20], who examined with difficulty the ability of colonies of European ants, such as *Myrmica rubra*, to acquire spatiotemporal learning. The variability between colonies led the author to conclude that ants could not acquire such learning (though for some colonies, under given circumstances, it was possible). We conducted similar experiments far later [13] and obtained evidence of spatiotemporal learning. Differences may thus exist in the behavioral and/or physiological reactions of different colonies of the same species and consequently in the observations made by different researchers working on the same species but on different colonies. Any study should preferentially be made on several colonies. However, generally, the results of different researchers are in agreement with one another, even if this is not detected at first sight due to the different protocols used by the researchers (Cammaerts, unpublished data).

Differences similar to those here observed between ant colonies also exist between other animal colonies, social groups or herds: some react more effectively; other less [12, 21]. Similar bee colonies maintained side by side present different functional patterns (e.g., M. Wollast, Bruxelles, personal communication). The bees of some of these colonies forage for longer time periods, collect nectar even when it is raining, collect more nectar than others during identical time periods, or work outside earlier at a lower temperature. Such differences between bees of similar colonies have also been reported by Kuppens [www.cari.be/medias/autres_publications/kuppens.pdf]. Since colony's functioning depends on its members' cognitive capabilities, the observation of differences between bees' capabilities leads to presume that bee colonies of the same origin, living in the same biotope, will differ as for their cognitive abilities. This has been reported by Seeley [22 and references therein], who even went a step further (see below).

Through a variety of mechanisms, the existence of valid ethological and/or physiological differences between colonies or groups of the same species may have an impact on the competition between these colonies or groups and ultimately on the evolution of the species. Indeed, Dall et al. [23] showed that individual differences can lead to different ecological states. Here, we experimentally demonstrated the existence of differences between colonies (a fact also reported by other researchers, e.g., [11]). Applying the idea of Dall et al. [23] to societies, it can be deduced that the greater a colony or group's ability to perform tasks, the higher their probability to enlarge, to produce descendants and to transmit their genotype. Let us now add the concept of Dawkins [24]. The phenotype of an individual can be extended to every function, including those of the nervous system, such as behavior, cognition, and those in relation with adaptation to the environment, which may lead to different evolutionary advantages. Applying this concept to colonies (which may differ as for their cognitive abilities [e.g., the present work]), it can be presumed that different colonies may possess different evolutionary advantages. Using the reasoning of Whener and Gehring [25], according to the groups' ethological abilities and capabilities in adequately reacting to their circumstances, some colonies (or social groups) may have a selective value, a fitness index (F) higher than those of other groups, i.e., a F value increased by a positive selective coefficient (+ s), while other colonies (or social groups) may have a value decreased by a negative selective coefficient (F – s). Briefly, on the basis of their ethological and/or cognitive abilities, some colonies (or social groups) may have a higher probability of transmitting their genotype. Even if based on the individuals' behavior, this is a fundamental trait of the evolution. To come back to Seeley [22] and to bees, this author explains throughout his book that social individuals' communication, efficiency in performing tasks, and social behavior in general influence the adaptation of the colony to its environment and impact the evolution of the species. As soon as in his introduction, the author writes: 'social insect groups are discrete groups and they possess variation, heritability, and fitness differences'. The above statement is also corroborated by the work of Anderson et al. [26].

The differences between colonies, which we have found to be reproducible and permanent, have, at least partly, a genetically origin and may have been brought by the founders through their genotype. Pruitt [27] has indeed stated that some behavioral traits of colony founders can affect the life of their colonies, and we have observed, while studying the ontogenesis of ants' cognitive abilities, that queens effectively possess different ability levels, with some queens reacting more effectively than others [2].

The 'social idiosyncrasies' previously considered by Mauss [28] are not exactly what we have observed. His concept is essentially the consequence of a culture, a civilization, and the customs of human communities. The present observations concern colonies or groups whose individuals can collectively use simple tools and methods and act according to hereditably acquired behavior. The 'social idiosyncrasies' considered by Mauss [28] concern populations of individuals able to use tools by themselves, improvise in new situations, and transmit their acquired knowledge to other individuals.

The present work is novel by its assessments of given traits in four similar colonies, demonstrating the existence of cognitive differences between such colonies. Similar studies should be conducted on other social species, such as other ant species, social bees, birds, rodents, and monkeys.

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DISCLOSURE

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About the Corresponding Author

Dr. Marie-Claire Cammaerts

Summary of background:
I work on ants since 1969, studying essentially their ethology and their physiology. I have examined their communication, recruitment strategies, areas marking, navigation systems, visual perception, conditioning abilities, among others. I have also studied the ontogenesis of some of their cognitive capabilities. More recently, I used ants as biological models for examining the effects of substances (drugs, food additives ...) consumed by humans. Until now, I could reveal the adverse effects of 21 such substances. Even if making pharmaceutical works, I go on studying the ants at an ethological and a physiological point of view, as proved by the present paper.

Current research focus:

- Effects of substances consumed by humans; the first to be studied are statins
- Ants' potential ability in learning, by operant conditioning, to perform initially unknown tasks
- Ants' potential instinctive perception of what is good or harmful to their health
- Impact on aquatic invertebrates of hormones nowadays present in natural water (using chironomes as models)

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