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Some New Information on Ants' Cemeteries Organization

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Author's contribution

The sole author designed, analyzed and interpreted and prepared the manuscript.

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ABSTRACT

Aim: We aimed to explain how ants manage to deposit nestmate corpses outside their nest.
Methodology: We first summarized a previous study of ours dealing with the subject, and reported others carried out in the meantime by other researchers. Then, we executed a new experimental work on the ant *Myrmica ruginodis.* We studied the ethological effects of chemical material present at cemetery sites and examined the tracks made by ants going to and from cemeteries. This gave the explanation of how and why ants transport and deposit corpses far from their nests, collectively or individually, and form piles or not.
Results: An ant loading a corpse moves away from its nest, discontinuously depositing some of the contents of its Dufour gland. It drops the corpse far from the nest, moves slowly, even rests for a time, and lays down some of its poison gland. Such deposits induce klinokinesis in nestmates and consequently incite nestmates carrying a corpse to approach this place moving slowly, sinuously, and finally to drop their load there, which leads to the formation of piles. When the ant has dropped the corpse, it returns to its nest while depositing, over a short distance, the trail of pheromone issued from its poison gland. Any ants can act similarly and individually. Corpses can thus be piled or laid down anywhere far from the nest.
Conclusion: The results of our experiment agree with other researchers' studies, and explain the apparition of piles of corpses, as well as the presence of corpses at places far from the nest.

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1. INTRODUCTION

Ants are eusocial insects (i.e. they cannot survive living alone), and perform numerous complex tasks resulting from individual simple acts and remarkable coordination between nestmates [1,2]. They build large nests, take care of their brood, and chemically mark the inside of their nest, nest surroundings, nest entrances, and foraging area [3]. They recruit nestmates for new food sources or nest sites using pheromones [2,3]. They also remove corpses and rubbish from their nests and transport the corpses quite far from the nest [4]. Indeed, dead ants and rubbish are generally found far from the nest, and are sometimes stacked at the boundaries of the ants' foraging area. Not removing dead ants and rubbish would lead to the development of moisture in the nest. Researchers have made observations on this important social task. Among others, Czechowski examined this trait in the ant *Myrmica schencki*, and presumed that the cemeteries may have a protective role for the colony [5]. Czechowski et al. [6] observed the content of *Formica polyctena* cemeteries and found not only dead workers but also mymecophiles. The latter can indeed be considered by ants as corpses of a given post-mortem age: according to Cammaerts [7], *Lasius flavus* ant workers locate the myrmecophilous beetle *Claviger testaceus* on larvae (nourished with dead insects), and either keep the beetle in the nest, or transport it onto the refuse. Haelewaters et al. [8] report that *Myrmica* ants do not remove dead workers from the nest during the winter, and that, during wintertime, the prevalence of ecto-parasitic fungi may increase. All these observations are in agreement with one another but do not explain how ants manage cemeteries, i.e. what is the ants' cemeteries organization. In 2009, we tried to understand how such 'cemeteries' could be formed, and our understanding was published in 2012, together with other works. Among these other works, was the use of adequate software allowing the analysis of animals' trajectories [9].

We recently reconsidered this topic. We reviewed the literature, made new observations, and carried out experiments using the ant *Myrmica ruginodis* (Nylander 1846) as a model to completely understanding how corpses are either randomly laid out of the nest or grouped in piles. Ultimately, we connected all the observations, experimental results, and modeling approaches to resolve the problem. In the present paper, our previous observations and those of other researchers on the subject ('Introduction' section) are summarized, our new work is presented ('Material and Methods' and 'Results' sections), and finally all the studies are connected, discussed, and a conclusion is given ('Discussion' and 'Conclusion' sections).

1.1 Literature Review

Myrmica ants, having found food or a new nest site, deposit a trail while returning to their nest [10]. They stop laying a trail when approaching the nest entrance. They might act similarly after having transported a corpse or rubbish far from their nest entrance. They logically move as far as they can, the farthest being the boundaries of their foraging area, and in a laboratory, the corners of the rectangular tray serving as a foraging area, and then they drop their load there. They may then rest a little, and thereafter return to their nest. At that moment, for a short distance, they may lay down some of the contents of their poison gland, i.e. the gland which produces the species trail pheromone. When approaching their nest, they forage as usual, without depositing a trail, using visual and/or olfactory cues [3].

In 2009, on the basis of the above reasoning, we observed the ant *Myrmica rubra* (Linnaeus, 1758) [9]. Pieces of extra strong white paper (1 cm^2) were deposited in ants' cemeteries over 8 days [3: Fig. 1A] and were then presented to the foragers, in their foraging area. The movement of these foragers was analyzed using relevant software [9] which is briefly explained below ('Material and Methods' section). The foragers were not attracted to the papers, but they moved with a higher sinuosity than usually. This suggested that the paper had been imbibed with the species trail pheromone, which is known to induce such locomotion [11]. The trail pheromone deposited by ants having dropped a corpse might induce, in other foragers carrying a corpse, a decrease in linear speed and an increase in sinuosity. This may incite them to stop, and drop the corpse. This was, of course, a preliminary approach to the 'cemeteries problem', and the aim was to evaluate the efficiency of the software which analyzed the trajectories [9].

Diez et al. [4] proved that ants loading a corpse never deposit a trail while moving away from their nest and when approaching a cemetery. It was also shown by the authors that foragers remember the place where they have laid down a corpse, and return to that place when transporting another corpse, particularly if the elapsed time between the two transportations was very short. It was also explained that piles of corpses are formed only when there are numerous corpses. Otherwise, corpses may simply be deposited on the boundaries of the foraging area. Obviously, all these observations and results are in agreement with our reasoning and first observations.

Wilson et al. [12] discovered that a dead ant is not immediately transported far from the nest but two days after the death, when the corpse still emits oleic acid but not the other substances produced while it was alive. We observed such a delay before the transportation of dead ants. We also noticed that very old corpses (more than one week old) are no longer transported far from the nest, probably because they no longer emit oleic acid.

1.2 Modelling Studies

The organization of cemeteries at a mathematical, modeling level, using the ant *Messor sancta* as a model was studied by Theraulaz et al. [13]. The apparition of cemeteries is a consequence of ‘local activation’ and ‘long range inhibition’ processes. This means that the presence of a corpse at some distance from the nest incites ants carrying a corpse to drop their load near the previously laid corpse, and that any corpse already dropped on a pile will no longer be transported by ants. This is a perfect explanation for the formation of piles of corpses. Nevertheless, such piles may never appear, and corpses may be separately laid far from the nest without being grouped (personal observation). Martin et al. [14] solved the latter problem. These authors proposed a different model explaining the clustering of corpses with a statistical effect, accounting for the formation of cemeteries around the ants’ area (which is an exact event and a personal observation), and in agreement with the fact that cemetery formation is not necessary a collective phenomenon but can be produced by a single ant (which is also a fact we observed).

2. MATERIALS AND METHODS

2.1 Collection and Maintenance of Ants

The experiments were done on four colonies of *M. ruginodis* collected in the Aise Valley (Ardenne, Belgium) in June 2016. The ants nested under stones; the colonies contained 500-800 workers, 1- 2 queens and brood. They were kept in the laboratory in artificial nests made of 1-3 glass tubes half-filled with water, with a cotton plug separating the ants from the water. 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. This 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* (Linnaeus, 1758) larvae provided as meat three times a week on a glass slide. The laboratory temperature was maintained at 18°C-22°C and the relative humidity at circa 80%. The lighting had an intensity of 330 lux while we cared for the ants and tested them. During other time periods, natural light was provided through a window, and varied from 5-120 lux according to the time of day. The ambient electromagnetic field had an intensity of 2-3 $\mu W/m^2$. The members of a colony are here referred as nestmates, which is the term commonly used by social hymenoptera researchers.

2.2 Obtaining Material Potentially Deposited at Cemetery Sites, Poison Gland Extraction, and Old Corpses

Six very small pieces of pure cotton were held with a pin, imbibed with pure hexane and each one was rubbed on the area of a cemetery. The six pieces of cotton were put into a glass tube (diam: 1 cm; height: 4 cm) into which 250 µL of hexane was then poured. This solution was kept at – 25°C. To examine the ants’ locomotion in the presence of such a solution, as well as the ants’ orientation towards it, 10 µL was deposited onto a piece of white paper (1 cm^2), and just after the evaporation of the hexane (one minute), this piece of paper was deposited in the ants’ foraging area, approximately in the center, and the ants’ trajectories were recorded and analyzed as explained below. To examine if the hexane solution of rubbed cotton induces trail-following behavior, 50 µL of the solution was deposited onto a circumference (R = 5 cm) drawn with a pencil on a piece of white paper and divided into 36 arcs of 10 angular degrees. After evaporation of the hexane, the piece of paper was deposited in the center of the ants’ foraging area, and the ants’ trail-following behavior was quantified as explained below.

Three workers' poison glands (the gland producing the species' trail pheromone), were isolated in 300 µL of hexane. To examine the ants' locomotion and orientation in front of such an extract, 10 µL (= 1/10 poison gland) was poured onto a piece of white paper (1 cm^2) which was then presented to the ants, in their foraging area, and their trajectories were recorded and analyzed as explained below. To quantify the trail-following induced by the solution of 3 poison glands in 300 µL of hexane, 50 µL of that solution (= 1/2 poison gland) was deposited onto a circumference (R = 5 cm) drawn with a pencil on a piece of white paper, in exactly the same way as to examine the trail-following induced by the solution of impregnated cotton, and the ants' reaction to the artificial trail was assessed as explained below.

The four colonies of *M. ruginodis* used were watched several times per day in order to spot the old corpses. Corpses present for about one week could be detected and were used for experiments. For doing one experiment, one old corpse was presented to the ants in their foraging area. Either the ants' locomotion in the vicinity of the corpses, or their orientation towards it was then assessed as explained below.

2.3 Analysis of Ants' Locomotion and Orientation

To analyze the ants' linear and angular speed, as well as to assess their orientation to a given object, 40 trajectories were each manually recorded on a glass slide horizontally placed above the ants' tray, a metronome set at 1 second allowing the assessment of the total time of each trajectory. Each trajectory was recorded until the ant reached the stimulus or walked for about 6 cm. The trajectories were then copied with a water-proof marker pen onto transparent polyvinyl sheets which were then affixed to a PC monitor screen. The trajectories were analyzed using specifically designed software [9], and each trajectory was entered into the software by clicking every 2-3 mm with the mouse and by then entering the location of the presented isolated worker's head. After that, the total time of the trajectory was entered, and the software was asked to calculate the ant's linear speed, angular speed, and orientation. The linear speed (V, here measured in mm/s) of an animal is the length of its trajectory divided by the time spent moving along this trajectory. The angular speed (i.e. the sinuosity, S, here measured in angular degrees/cm) of an animal's trajectory is the sum of the angles, measured at each successive point of the trajectory, made by two successive segments divided by the length of the trajectory. The orientation (O, here measured in angular degrees) of an animal towards a given object (here an impregnated piece of paper) is the sum of the angles, measured at several successive points of the recorded trajectory, made by each segment 'point i of the trajectory - given object' and each segment 'point i - point i + 1', divided by the number of measured angles. When O is less than 90°, the animal has a tendency to orient itself towards the point; when it is greater than 90°, the animal has a tendency to avoid the point. Each distribution of 40 values was characterized by its median and quartiles (Table 1) and distributions of the same variables could be compared to one another using the non-parametric χ^2 test [15]. Control values were obtained by presenting pieces of blank paper to the ants, then recording and analyzing 40 trajectories.

2.4 Assessment of Ants' Trail-following Behavior

As stated above, to perform one experiment, 50 µL of the solution to be examined was deposited on a circumference (R = 5 cm) drawn with a pencil on a piece of white paper and divided into 36 arcs of 10 angular degrees. The deposit was made using a metallic normograph pen. One minute after, the piece of paper was placed in the ants' foraging area. The response of 40 ants to the circumference was assessed by the number of arcs of 10 angular degrees they walked without departing from it, even if they reversed their walking. If an ant turned back when coming in front of the circumference, its response was assessed as 'zero arc walked'; when an ant crossed the circumference without following it, its response equaled 'one walked arc'. Control numbers were obtained by presenting blank circumferences to the ants. The distributions of values were characterized by their median and quartiles (Table 1), and were compared to one another using the non-parametric χ^2 test.

2.5 Obtaining Ants' Tracks on Smoked Glass

Cover glasses were smoked, held with a forceps, and were, after 5 minutes, deposited on ants' cemeteries sites. They were removed as soon as one ant had walked on it, either coming to or going away from the cemetery. The direction of the ants was noted. The used smoked glass was deposited on a glass set 10 cm above a piece of white paper. It was photographed in ‘macro’ mode. The presence of either very short tracks or long, continuous ones between those made by the ants’ tarsi (extremities of their legs) was noted and correlated with the direction the ants had walked on the smoked glass (towards or away from the cemeteries).

3. RESULTS

3.1 Observation of Ants Transporting a Corpse Far from the Nest

Several ants transporting a corpse far from the nest, dropping it, and then returning to near the nest, were observed (Fig. 1A, B, C). While moving far from the nest, ants holding a corpse only very briefly and shortly touched the ground with the tip of their gaster. After having dropped the corpse, the ants generally stopped for a few minutes, and touched the ground with the tip of their gaster. They then moved slowly, near the corpse. After that, the ants moved towards the nest, almost continuously touching the ground with the tip of their gaster. They did this for 5-10 cm. When walking closer to the nest, they moved more quickly and no longer touched the ground with the tip of their gaster. Such a sequence of behavior always occurred, whether there was a pile of corpses or not.

3.2 Linear and Angular Speed in Front of Material Collected from Cemetery Areas, and in Front of Ants’ Poison Gland Extract

Ants’ trajectories were recorded in the vicinity of a blank paper, of a paper imbibed with material collected from cemeteries, and of a paper imbibed with an extract of the species’ poison gland (the source of the trail pheromone) looking at the ants, and thus being not blind to the situation. After this, the trajectories were analyzed using relevant software this time being blind to the situation. The assessed ants’ linear and angular speeds are given in Table 1. It appeared that, in front of the material collected in cemeteries, the ants moved at a lower linear speed and with a higher angular speed than when being near a blank paper. These differences were significant: linear speed: χ^2 = 43.69, df = 2, *P* = 0.001; angular speed: χ^2 = 58.38, df = 1, *P* = 0.001. An extract from the poison glands also induced such locomotion differences, i.e. the ants moved more slowly and more sinuously. The material present in cemeteries seemed thus to have a behavioral effect similar to that of a poison gland extract. It even had a stronger effect than the poison gland extract used (which corresponded to a 1/10 poison gland): linear speed: 9.9 *vs* 10.6 mm/sec, χ^2 = 1.27, df = 2, *P* = 0.70; angular speed: 198 *vs* 177 ang. deg./cm, χ^2 = 8.77, df = 2, *P* = 0.02.

3.3 Orientation to Material Collected from Cemeteries, and to Ants’ Poison Gland Extract

The numerical results (obtained being blind to the kind of analyzed trajectories) are given in Table 1. The ants did not orient themselves towards a blank paper, nor towards a paper imbibed with cemeteries’ material, and nor towards a paper imbibed with poison gland extract, and the median values obtained for the two latter objects are very similar (76.5 and 77.0 ang. deg respectively *vs* control: 81.8 ang. deg.). The ants approached the cemeteries’ material (Fig. 1D) just like they approached the poison gland extract due to their increase in sinuosity and decrease in linear speed, thus performing some klinokinesis. The statistical results were: cemeteries *vs* control: χ^2 = 0.84, df = 2, *P* = 0.70; cemeteries *vs* poison gland: χ^2 = 0.55, df = 2, *P* = 0.80. Such a result showed once more that the material lying in cemeteries had a behavioral effect similar to that of a poison gland extract.

3.4 Ants’ Locomotion Near, and Orientation to, an Old Corpse

The numerical results (obtained being blind, and given in Table 1) confirmed what could be seen while carrying out the experiment. In front of an old corpse (a corpse being more than one week old), ants presented no reaction at all: they did not move more slowly or quickly, they were not attracted by the corpse, and they did not hold the corpse nor transport it. The values of ants’ linear speed, angular speed, and orientation obtained for such an old corpse were perfectly similar to the control ones: respectively 14.5 *vs* 14.8 mm/sec, 111 *vs* 118 ang. deg. /cm, 81.2 *vs* 81.8 ang. deg. Having obtained these results being blind, we can affirm that an old corpse induced no reaction in ants.

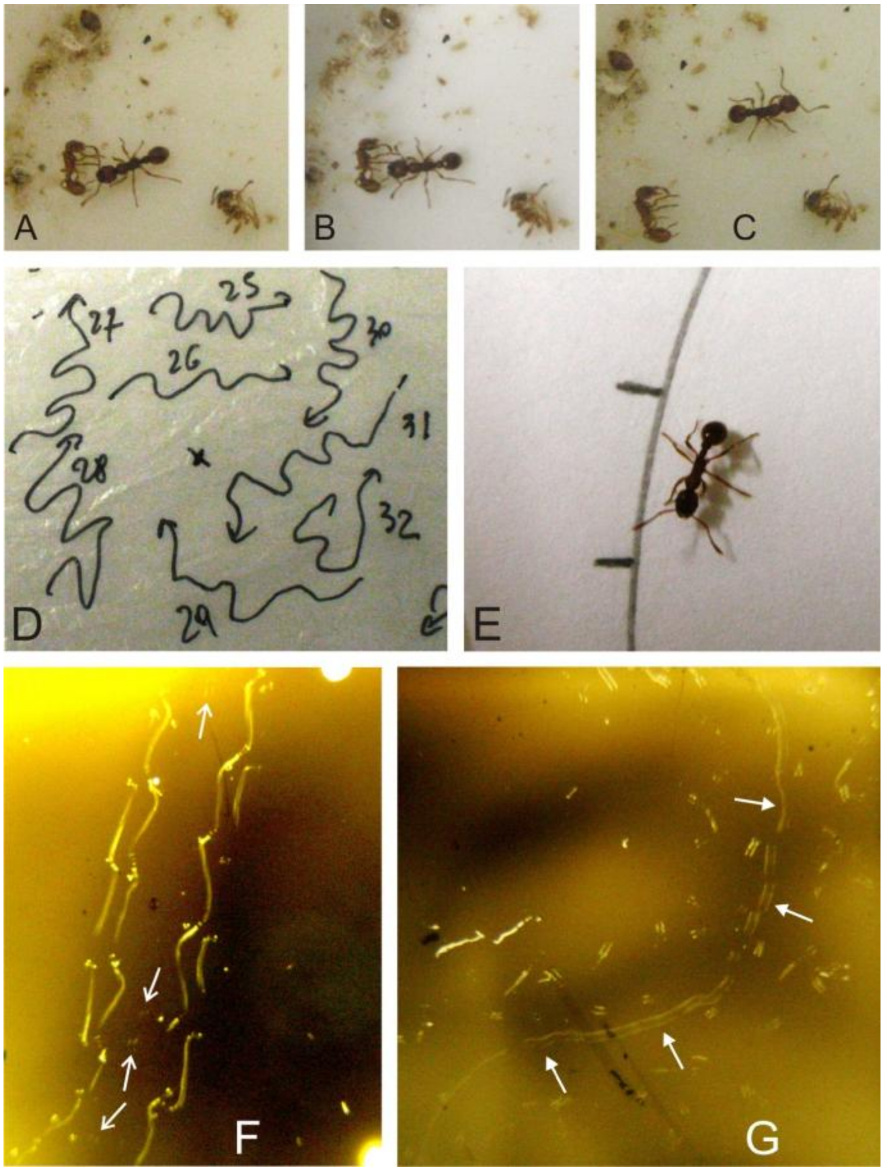

Fig. 1. Some views of the experiment. A: An ant having just dropped a corpse; its gaster is rather horizontal. B: The same ant resting after having dropped the corpse; its gaster is curved towards the ground. C: The ant leaving the place where it has dropped the corpse; its gaster is rather vertical, tilted towards the ground: the ant is depositing a trail. D: Recorded trajectories of ants in the vicinity of material collected in cemeteries (indicated by a cross); the ants do not really orient themselves towards the collected material; they approach it moving sinuously and slowly, thus making some klinokinesis. E: An ant following a circular trail traced with an extract of material collected in cemeteries; these sites are thus covered with very small amounts of the ants' trail pheromone, a substance produced by the poison gland and deposited by the ants with the tip of their gaster (cf photo C). F: Tracks left on smoked glass by an ant transporting a corpse and moving towards the boundary of its foraging area. The ant deposits very small spots of the content of its Dufour gland, which makes short tracks (indicated by white arrows) between longer ones made by its legs. G: Tracks left on smoked glass by an ant having dropped a corpse and coming back to its nest. The ant touches the ground with the tip of its gaster, making long tracks (indicated by white arrows) between smaller ones made by its legs. It deposits a trail

Table 1. Ants' linear and angular speeds, orientation, and trail-following induced by blank paper (control), by chemical material collected in cemeteries, by a poison gland extract, and by a corpse present in the foraging area for at least one week (old corpse). Experimental details and statistics are given in the text. Briefly, the chemical material collected in the cemeteries induced reactions similar to that induced by a poison gland extract. Ants dropping a corpse may thus deposit this secretion (containing their trail pheromone). A corpse lying outside of the nest for one week induced no reaction; it will therefore stay where it is. It would be irrelevant to examine if such an old corpse could induce trail-following

Experiments, extract or object	Linear speed mm/sec	Angular speed ang. deg./cm	Orientation ang. deg.	Trail-following n° walked arcs
Control	14.8(13.2-16.3)	118 (94-129)	81.8(62.8-96.9)	1.0 (1.0-1.0)
Cemeteries	9.9(9.0-12.0)	198 (171-219)	76.5(62.6-94.7)	3.0 (2.0-5.0)
Poison gland	10.6(9.5-11.6)	177 (168-194)	77.0(64.9-93.9)	3.0 (2.0-4.0)
Old corpse	14.5(12.8-15.9)	111 (90-122)	81.2(57.7-95.6)	

3.5 Trail-following Induced by Material Collected from Cemeteries, and by a Poison Gland Extract

The numerical results can be found in Table 1. Of course, the ants did not follow a blank circumference. On the contrary, they followed a circumference imbibed with material collected in cemeteries (Fig. 1E), and this result was significant: $\chi^2 = 39.60$, df = 1, $P = 0.001$. The ants similarly followed a circumference imbibed with a poison gland extract (corresponding to ½ poison glands). The median values obtained for the cemeteries and for the poison gland extract equaled 3.0 walked arcs of 10 degrees; they did not statistically differ: $\chi^2 = 2.91$, df = 2, $P = 0.30$. This similarity once more revealed an identity between behavioral effects of cemeteries material and of poison gland extract.

3.6 Ants' Tracks on Smoked Glass

For the six cemeteries we had at our disposal, we always obtained the same ants' tracks on smoked glass. When ants moved towards the cemeteries, they left only very short, spaced tracks with the tip of their gaster (Fig. 1F). Such tracks showed that these ants going to cemeteries deposited discontinuously the content of their Dufour gland [16]. When ants moved away from the cemeteries, they made long, continuous, large tracks with the tip of their gaster (Fig. 1G). Such long tracks revealed that these ants returning from cemeteries deposited nearly continuously (at least at the beginning of their displacement) the content of their poison gland [16]. This last deduction is in agreement with the results in paragraphs 3.1, 3.2, 3.3, and 3.5 of the results section.

4. DISCUSSION

On the basis of the behavior of ants transporting corpses to cemeteries, of ants' behavior in front of material collected in cemeteries (linear speed, angular speed, orientation, trail following), and on ants' tracks left on smoked glass when going to and returning from cemeteries, the ants' usual behavior in relation to the removal of dead nestmates could be described. Only the removal of corpses and no longer that of refuse was examined, as the two elements appeared to be treated in different ways. This has also been noted by Banik et al. [17]. The ants transport a corpse out of the nest, and move far from it without trailing, but from time to time deposit some of their Dufour gland. They usually make such a deposit in order to reinforce the marking of their foraging area [2,3]. They drop the corpse at the boundary of their foraging area, rest a little, and deposit some of their poison gland there. Such deposits increase the sinuosity and decrease the linear speed of other workers carrying a corpse; these workers will thus stay and lay down their load. After having dropped a corpse, the ants return to the nest, depositing continuously their trail pheromone over a short distance, and stop trailing when approaching the nest. This occurs in the presence of corpses of about 2 days old [12], when they chiefly emit oleic acid and no longer the substances usually produced by live ants. We showed that after a long period (one week), the corpses no longer induce any reaction in the ants. Diez et al. [4] demonstrated that ants holding a corpse never deposit a trail when walking towards a cemetery. These authors also revealed individual behavior, i.e. memorization of the place where they previously went to deposit a corpse. They also explained that no piling occurs when only a few corpses exist; the latter are transported out of the

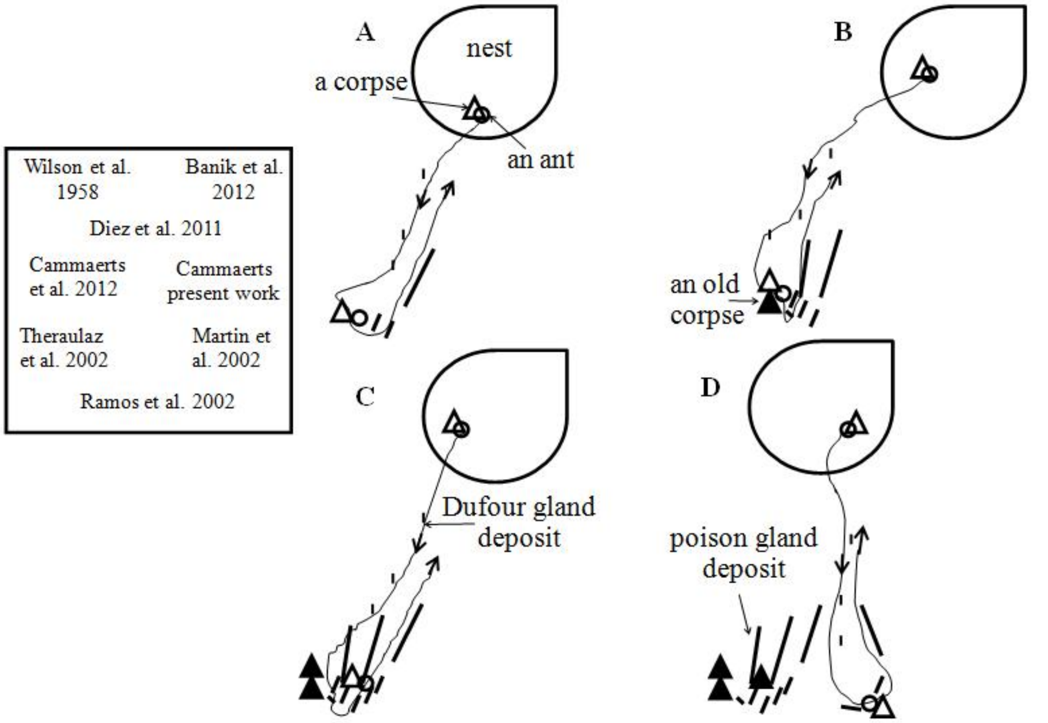

Fig. 2. Transportation of corpses and cemeteries formation, schematized on the basis of the eight works cited on the left of the schema. A: An ant, perceiving a corpse (of about two days old) in the nest, transports it far from the nest, discontinuously depositing an amount of its Dufour gland. The ant then drops the corpse, rests, and lays down some very small amounts of its poison gland. It then returns to its nest depositing, over a rather short distance, its poison gland content again, this time nearly continuously, and this deposit now acts as a trail pheromone. B: another ant acts similarly, B, C: The secretion deposited after a corpse is dropped incites other ants carrying a corpse to move to the location slowly and sinuously, and finally to also drop their load in the vicinity of the previously dropped corpses. D: Of course, other ants may move from the nest in another direction, and drop corpses elsewhere. B, C, D: contrary to recent corpses, old ones (i.e. of at least one week old) induce no reaction in ants; they therefore stay in place, isolated, or grouped

nest, far from it, and simply dropped anywhere. Theraulaz et al. [13] explained, by modeling the ants' behavior, how piles can be formed when numerous corpses exist: there is successively a 'local activation' (the ant drops the corpse where a corpse is already present) and a 'long range inhibition' (the already laid corpses are no longer removed by the ants). Similar modeling was also reported by Ramos et al. [18]. The above summarized modeling found a biological explanation in the present work. A pile can be formed because the poison gland deposit, made by ants dropping a corpse, decreases the ants' linear speed and increases their angular speed, thus inducing some klinokinesis, which brings ants closer to the gland deposit. As often in such cases, an iterative event takes place: the more ants that come, the more deposits are made, and consequently even more ants will come. Moreover (see above), old corpses no longer induce any transport behavior; they thus stay in the cemetery. However, piles are not necessarily formed. Martin et al. [14] explained the clustering of corpses by a somewhat different model, including statistics, which could account for the location of corpses all around the ants' foraging area and for the fact that one individual can by itself create a cemetery. Let us add that we also, but seldom observed moribund ants moving with difficulty far from the nest and dying, alone, on the foraging area. This has also been observed by Heinze and Walter [19].

The present work has been done on *M. ruginodis*. The here given updated description of ants' cemeteries organization is, of course, more complete but not in contradiction with the pioneer one made by Howard and Tschinkel in 1976, in *Solenopsis invicta* [20]. It should be of interest to study similarly the cemeteries' organization in other ant species, above all in species not using or scarcely using a trail pheromone. Ants are spectacularly expert in cleaning their nest and transporting corpses and refuse far from it, sometimes piling them. However, they are not the only animals to do so. Bees also transport corpses and refuse away from their hives. Termites also present necrophoric behavior [21] and several birds and mammals also do so [22]. It would be interesting to examine the process of this behavior, as well as its ontogenesis and its evolution. In ants, only the oldest ants transport corpses far from the nest (personal observation); callow or young ants must thus 'learn' how to do so. Such 'learning' can take place only after the ant has acquired the knowledge of its foraging area, nest vicinity, nest entrance, as well as of the species trail and foraging area marking pheromones.

5. CONCLUSIONS

The ants' cemeteries' organization is the following. A corpse of at least two days is transported by an old ant far from the nest, up to the boundaries of the foraging area. While doing so, the worker lays down some spots of its Dufour gland content which reinforces the marking of the traveled area. Far from the nest, the corpse is dropped. The worker stays there a moment and lays down some of its poison gland. These deposits induce nestmates to stay in the vicinity of the corpse that was dropped. This promotes other workers to drop the corpses they may have transported there. After having dropped its load, the ant returns to its nest, laying down, over a short distance, the trail pheromone issued from its poison gland. The other ants loading a corpse act similarly, moving in any direction. This explains the presence of corpses at any place far from the nest. However, since the pheromonal deposits made by ants dropping a corpse incite congeners to move to the location slowly, sinuously, and consequently to drop their load there, piles of corpses may form. This story is in agreement with all the experimental and mathematical studies already done on the subject.

COMPETING INTERESTS

Author has declared that no competing interests exist.

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