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Research article

How temperature influences displacements and corpse aggregation behaviors in the ant *Messor sancta*

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Abstract. We studied the effects of temperature on movement and individual corpse aggregation behaviors (picking up or dropping a corpse) in the ant *Messor sancta*. Dispersion of ants in space was higher at 30 °C than at 16 °C. Concerning aggregation behaviors, we observed at both temperatures that the probability of picking up a corpse from a pile was negatively correlated with pile size, while the probability of dropping a corpse was positively correlated with pile size. The combined picking up and dropping behaviors represent a local amplification of corpse aggregation that is stronger at 30 °C than at 16 °C. Overall, this study shows clearly that the transport of corpses by ants, as well as the amplification process involved in corpse aggregation, is modulated by temperature. The implications of these results on the dynamics of ant cemetery formation (and other aggregation behaviors) are discussed. We propose that the modulation of a local amplification process by an environmental factor could be a general mechanism involved in the coordination of ant activity to adapt the external and internal shape and organization of the nest to environmental conditions.

Keywords: Temperature, displacement, corpse aggregation, ant cemetery, *Messor sancta*.

Introduction

In social insects, aggregation of nest material is at the basis of collectively built impressive structures whose size dwarves the individual workers (Grassé, 1984; von Frisch 1974; Camazine et al., 2001; Tschinkel, 2004). Thus, understanding the individual behaviors involved in aggregation phenomena in general can be a first step towards understanding how these highly complex structures and their regulation emerge. An important step is also to understand the impact of environmental factors, such as temperature, on these behaviors (and thus indirectly also on the resulting structures). For example, the shape and structure of an ant nest can be modified according to the variations of environmental temperature (Wilson, 1971; Frouz, 2000; Banschbach et al., 1997) in order to create a regulated microclimate. Several studies have demonstrated the ants' ability to detect local differences in temperature, e.g. workers of *Atta* sp. can choose a location at the optimal temperature for their brood (Bollazzi and Roces, 2002) and the castes of several species show thermal preferences (Banschbach et al., 1997; Ceusters, 1986) that may also be linked to their internal migration-hibernation-reactivation activity cycle (Billen, 1984). This thermal sensitivity could intervene in the individual coordination mechanisms involved in aggregation processes. For example, a temperature gradient could give rise to spatial preferences in the place where aggregation is initiated, which could explain the adaptive responses to temperature variations observed in many ant species.

In this work we investigated how temperature can modify individual aggregation behavior in social insects taking as an example the corpse aggregation phenomena observed in the ant *Messor sancta*. This species, as many other ant species (Hölldobler and Wilson, 1990), is known to take the corpses of dead workers out of its nest and to deposit them together in what is frequently termed a cemetery (Theraulaz et al., 2002). The individual behaviors involved in this activity are: picking up a corpse, carrying it and, finally, dropping it at some place. Cemetery formation in the ant *Messor sancta* was chosen as an experimental paradigm of aggregation processes in general because its dynamics was recently shown to be of the Turing pattern formation type (Theraulaz et al., 2002), a general class of self-organized

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mechanisms that can potentially explain a large range of phenomena involved in pattern formation and morphogenesis (Turing, 1952; Camazine et al., 2001). By a combination of experimental and modeling techniques, Theraulaz et al. (2002) have been able to explain the dynamics of cemetery formation as the outcome of two basic mechanisms: a) a local amplification process, where ants show a tendency to pick up corpses preferentially in areas of low corpse density and to drop them in areas of high density, and b) a "competition" process between corpse piles in formation, i.e. the dissolution of smaller piles to the profit of larger piles. The result is symmetry-breaking and the formation of regularly spaced corpse piles. In this paper we investigated whether temperature can interact with the amplification and competition processes described above and whether it can influence aggregation processes in general. We studied in particular the effects of temperature on: (i) the characteristics of ant's movements (because in aggregation phenomena, variations in the movement characteristics of individuals can have important consequences on the final structure obtained, Bonabeau et al., 1998) and (ii) the probability of occurrence of the two individual behaviors involved in the dynamics of corpse aggregation, i.e. picking up and dropping corpses.

Material and methods

Studied species

Experiments were performed from March to June 2002 with a colony of the Mediterranean seed-harvesting ant *Messor sancta* Forel (Myrmicinae). This species has an intermediate polymorphism with body length between 3 and 9 mm (Cerdan, 1989). In their natural environment *M. sancta* colonies can reach several thousands individuals. A colony collected near Narbonne (Languedoc-Roussillon, France) was maintained in a 40×30 cm plastic box coated with Fluon® to prevent ants from escaping. Ants were given water in the form of moist cotton and fed *ad libitum* with seeds, a solid mixture of carbohydrates, vitamins and eggs (Bhatkar and Withcombs, 1970) and maggots.

Experimental set-up

Ants were filmed (SONY DCR-VX2000E) while moving on a white thermo-controlled table linked to a thermocryostat (combination of a thermostat and a cryostat: temperature is controlled by the combined effect of heating and cooling). This table is connected by 20 thermo-sensors to a temperature acquisition unit (HP 34970A) in order to control and monitor its temperature. The table was surrounded by white sheets to homogenize light and to mask any visual landmarks. After each experiment the table was cleaned with alcohol to remove any chemical cues. The experimental colony (containing several hundred workers) was placed beneath the table and ants could access the table spontaneously along a small wood stick placed in a hole in the center of the table. On the table an arena (50 cm in diameter and 10 cm in height) confined ants' movements. Experiments were done in a room with constant temperature two degrees above the table temperature. This difference is favorable (S. Blanco and R. Fournier, pers. comm.) to produce a stable situation with limited convective flows between the room and the table. The relative humidity of the room was maintained around 50%.

  M. sancta ants tolerate a large range of temperature conditions: Cerdan (1989) observed foraging activity for ground surface temperatures as low as 12 °C in autumn and spring and as high as 35 °C in sum-

mer, while Cerdá et al. (1998) observed the greatest foraging activity for a soil temperature of 30 °C in *Messor bouvieri* (= *Messor sancta* according to Bernard, 1968). In our study we will thus use temperatures in this range: 16 °C (Group 16), 25 °C (Group 25) and 30 °C (Group 30) for individual movement and 16 °C and 30 °C for picking up and dropping corpses behaviors.

Path analysis

We concentrate in this study on the displacement of solitary individuals. Since *M. sancta* movement is known to change when workers are moving solitarily or in a group (Fourcassié et al., 2003) the wood stick was removed immediately after the first ant arrived on the table. Recording was stopped either just before the ant reached the border of the arena or after one minute. After each trajectory, the ant just tested was removed from the colony to prevent being re-used in the next trajectory recording. Paths were digitized with the video-tracking software Ethovision® (version 1.90, Noldus Information Technology, http://www.noldus.com/products/index.html) on the plain surface. Given the average speed and the average ant size (around 5 mm length), fixes were recorded once every second (≈ 2.6 body lengths, see Tourtellot et al., 1991). Twenty-five trajectories of single ants walking in the empty arena were videotaped for each temperature.

  For each thermal condition we analyzed each trajectory individually. We first computed the speed of each trajectory (travel distance divided by travel time, cm/s). The geometry of the trajectories was characterized by a series of free paths and turning angles α_i (rad) between them (Fig. 1). We started a new free path l_i when the directional change β_i (rad) of a segment of trajectory (from the beginning of the current free path to the current fix) with respect to the last free path exceeded 0.175 rad (10 degrees, see Fig. 1a). Free paths of length less than 5 mm (one individual length) were not considered. This procedure permits to remove artificial turns due to pixel size while conserving the general shape of the trajectory (Turchin, 1998). The mean free path l represents the mean straight distance walked by ants before a significant directional change occurs. It
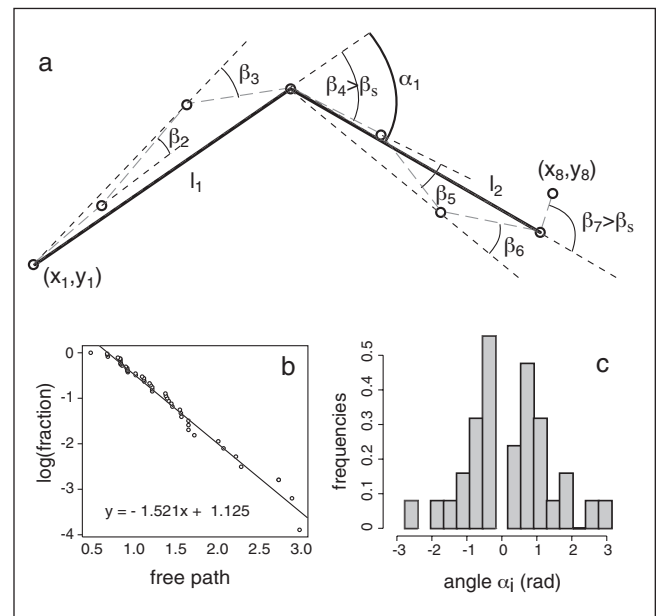

Fig. 1. Path analysis. (x_j, y_j) are *M. sancta* positions at time t_j. (a) The path is decomposed into free paths l_i and turning angles α_i between them. A new free path is started whenever the turning angle β_i exceeds β_s (= 0.175 rad). (b) Log survival curve of the measured free paths of one trajectory at 25 °C. (c) Phase function with a forward tendency ($g = 0.69$) of one trajectory at 25 °C.

was estimated as the inverse of the slope of the log-linear survival curve of the free paths l_i (see Fig. 1 and Haccou and Meelis, 1992).

The probability density function Φ of the turning angles (also called phase function, between $-\pi$ and $+\pi$) was determined for each temperature condition. From this angular distribution, the anisotropy coefficient g was computed to give an estimation of the tendency to move in the same direction:

$$g = \int_{-\pi}^{\pi} \phi(x)\cos(x)dx \; ; \; g \in [-1;1]$$

A uniform phase function (ants have the same probability to make angular changes in any direction) corresponds to isotropic diffusion with $g \approx 0$. When g is close to +1, ants have a high tendency to move forward. A value of g close to -1 indicates frequent reversal of direction.

Speed v, mean free path l and anisotropy coefficient g can be summarized in the diffusion coefficient D:

$$D = \frac{l*v}{2}$$

$$l* = \frac{l}{1-g}$$

($l*$ is called the mean free transport path). D represents the space visited by ants per unit of time and completely characterizes the diffusive nature of ant dispersal.

Picking up and dropping behavior

The second part of the individual behavior study consists in the quantification of temperature effects on corpse aggregation, which involves two behaviors: picking up a corpse and dropping a corpse. Corpse piles were formed artificially in the arena. Experiments were done at two temperatures (16 °C: Group 16, and 30 °C: Group 30) with four different pile sizes: a single corpse (pile size = 1, Ø = 0.3cm) and piles of size 10 (Ø = 0.9), 50 (Ø = 1.7cm) and 200 corpses (Ø = 3.8cm). In the single corpse experiments 30 corpses were placed in form of a 5 cm square grid. For piles of 10 and 50 corpses, eight piles of the fixed size were placed at equal distance (5cm) from the center of the arena. For the last size (200 corpses) only four piles were made at a distance of 5cm from the center of the arena due to the large diameter of the piles. In each thermal condition, two series of experiments were made, the first aimed at studying the picking up behavior (three experiments of one hour, continuous recording) and the second aimed at studying the dropping behavior (three experiments of four hours, continuous recording). In the dropping experiments isolated corpses were also placed along the arena walls to decrease the probability for ants to pick up corpses from the piles. In each picking up and dropping experiment, the ant nest was always connected to the table and all the ants of the colony can climb on the platform via the wood stick and interact freely with the corpse piles. All experiments were recorded on video and we counted afterwards all physical contacts between ants and piles. When a corpse was dropped or picked up on a pile of size 1 or 10, the data ceased to be collected on this pile because this represented a considerable change in the pile size.

The numbers of picking up (N_p) and dropping (N_d) of corpses on piles, the number of contacts between workers which did not transport a corpse and the piles (N_c) and the number of contacts between workers which transported a corpse and the piles (N_{ct}) were counted. The probabilities of an individual to pick up and to drop a corpse on a pile were studied in relation to table temperature and as a function of the pile size.

Probability of picking up: $P_p = N_p / N_c$
Probability of dropping: $P_d = N_d / N_{ct}$

Statistical analysis

In the path analysis, the speed, the mean free path, the anisotropy coefficient g and the diffusion coefficient were computed for each trajectory.

The normality of the data distribution was tested with a Shapiro test and homoscedasticity with a Bartlett test. When normality and homoscedasticity were not rejected an ANOVA followed by a Tukey honestly significant differences post-hoc test (TukeyHSD) were performed. Otherwise we used the non-parametric Kruskal-Wallis test to analyze the overall effect of temperature and the Nemenyi post-hoc (Zar, 1999). The Kolmogorov-Smirnov test (KS test) was used to compare the phase functions pooled over all trajectories between the three temperatures. In all tests, we set $\alpha = 0.05$ (with a Bonferroni correction in the KS test).

In the picking up and dropping analysis, all probabilities were compared two by two with a proportion test based on a normal approximation (Prop.test function in the R statistical software) with a Bonferroni correction in the case of multiple comparisons.

All statistical analyses were done in the R statistical software (http://www.r-project.org/, version 1.7); the R code can be requested from the authors.

Results

Path analysis

Figure 2 summarizes the ant speeds at the different temperatures. Median speed changes from 0.80 cm/s at 16 °C to 1.14 cm/s at 25 °C and to 1.50 cm/s at 30 °C. Temperature has clearly an effect on speed: when temperature increases, the ants' running speed increases as well (Kruskal-Wallis, $H = 37.38$, $df = 2$, $p < 0.001$). Significant differences (Nemenyi test) are observed between Group 16 and Group 25 and between Group 16 and Group 30.
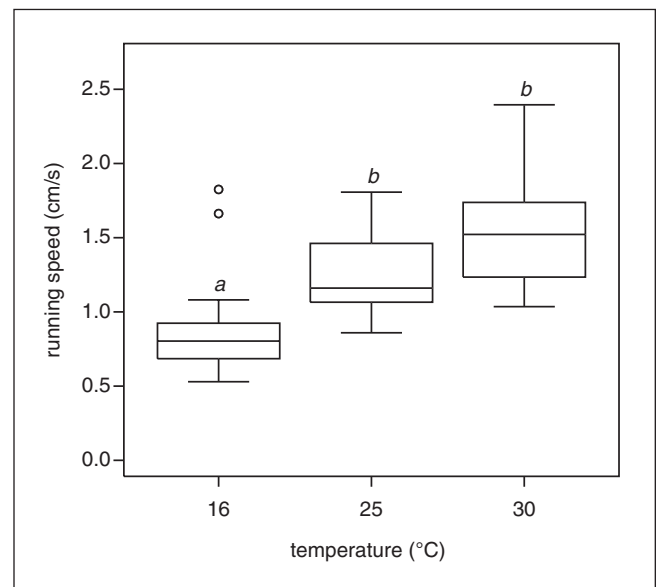
Fig. 2. Effects of temperature on ant speed. Boxplots of *M. sancta* speed as a function of temperature. The line within the box indicates the median and the lower and upper boundaries of the box are the first and third quartiles (Dalgaard, 2003, p65). The whiskers show the largest and smallest observations that are not considered to be outliers. The additional points are considered "extreme" values and are shown separately. Data were analyzed with a Kruskal-Wallis test followed by a Nemenyi test (a and b indicate different statistical populations with p < 0.05). $n = 25$ for each group.

The positive relationship between temperature and mean free path l is shown in Figure 3. The median mean free path increases from 0.602 cm at 16 °C to 0.710 cm at 25 °C and to 1.022 cm at 30 °C. There is a significant effect (Kruskal-
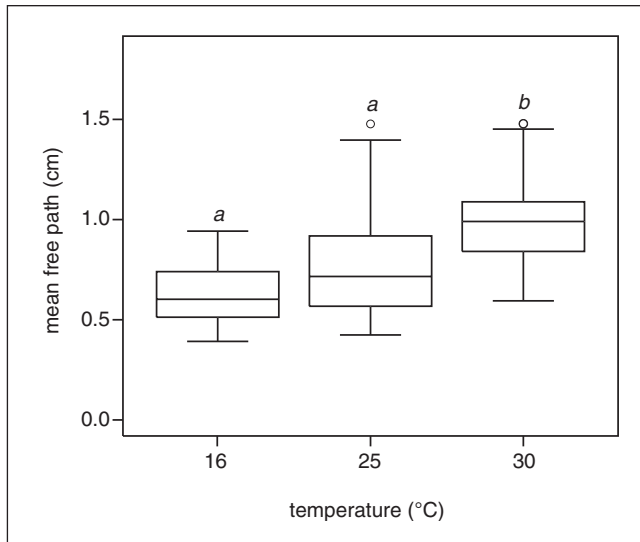

Fig. 3. Effects of temperature on the mean free path. Boxplots of *M. sancta* mean free paths as a function of temperature. Data were analyzed with a Kruskal-Wallis test followed by a Nemenyi post-hoc test (see legend figure 2 for more details on statistical notation). $n = 25$ for each group.
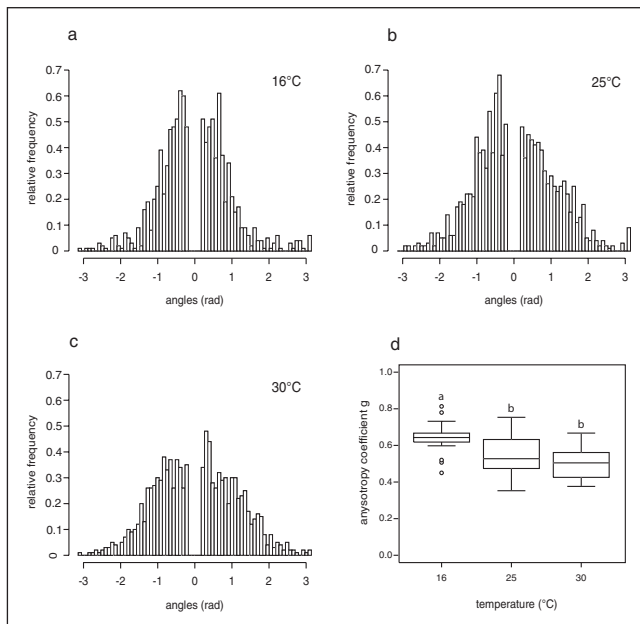

Fig. 4. (a, b, c). Effects of temperature on the phase function. Phase functions (histograms of turning angles pooled over all trajectories) of *M. sancta* ants for the three studied temperatures. Relative frequencies are on the Y-axis and angle values (rad) on the X-axis. **(d).** Effects of temperature on the anisotropy coefficient. Boxplots of *g* of *M. sancta* ants as a function of temperature. The data were analyzed with an ANOVA followed by a TukeyHSD post-hoc test.

Wallis test, $H = 25.34$, $df = 2$, $p < 0.001$). Group 30 is significantly different (Nemenyi test) from both group 16 and group 25.

Figure 4 shows the angle distributions and *g* values for the three studied temperatures. For the phase function, Group 16 is significantly different from Group 25 (KS test, $D = 0.096$, $p < 0.01$) and Group 30 (KS test, $D = 0.177$, $p < 0.001$). No difference is found between Group 25 and Group 30 (KS test, $D = 0.037$, $p = 0.411$). These results are confirmed with the median *g* values which decrease with increasing temperature from 0.643 at 16 °C to 0.530 at 25 °C and to 0.505 at 30 °C (ANOVA, $F_{2, 72} = 16.65$, $p < 0.001$). Group 16 is significantly different (TukeyHSD) from Group 25 and Group 30. All phase functions are forward oriented ($g > 0$, which corresponds to a correlated random walk) and this tendency decreases with increasing temperature.

Figure 5 shows the overall impact of temperature on the diffusive dispersal of ants: D increases with temperature. The median diffusion coefficient increases from 0.685 cm²/s at 16 °C to 1.001 cm²/s at 25 °C and to 1.436 cm²/s at 30 °C. There is a significant effect of temperature on D (Kruskal-Wallis test, $H = 20.89$, $df = 2$, $p < 0.001$). Group 16 is significantly different from both Group 25 and Group 30 (Nemenyi test). These results show that dispersion in space and time increases with temperature: in the same time, ants visit more space at 30 °C than at 16 °C.

Picking up and dropping behavior

Figure 6a shows the picking up probabilities as a function of pile size and temperature. At 16 °C, the picking up probability
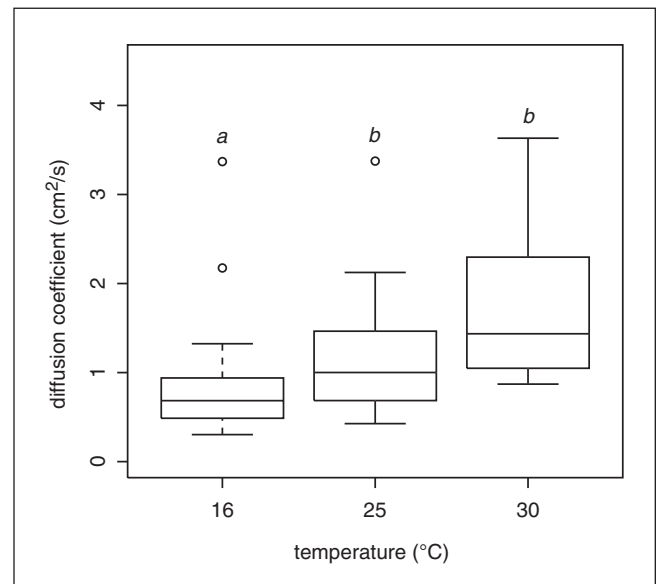

Fig. 5. Effects of temperature on the diffusion coefficient. Boxplots of *D* of *M. sancta* as a function of temperature. The data were analyzed with a Kruskal-Wallis test followed by a Nemenyi post-hoc test (see legend of figure 2 for more details on statistical notation). $n = 25$ for each group.
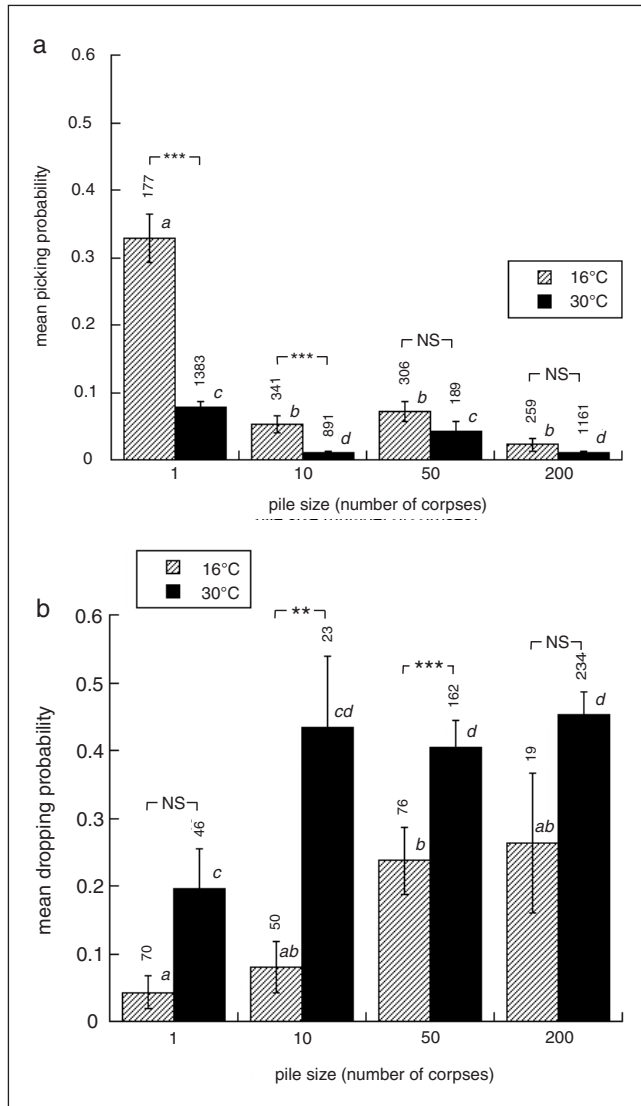
Fig. 6. (a) Picking up probabilities P_p of *M. sancta* as a function of the size of corpse piles and of temperature. **(b)** Dropping probabilities P_d of *M. sancta* as a function of the size of corpse piles and of temperature. Probabilities are represented with their standard errors. The number of contacts with piles is indicated above the error bar. Statistically significant difference between pile sizes are indicated by *a* and *b* for 16°C ($p < 0.01$), and by *c* and *d* for 30°C ($p < 0.01$). The bars bearing the same letter are not significantly different at the 5% level. For the comparisons between both temperatures, differences are indicated by ✳✳ when $p < 0.01$, by ✳✳✳ when $p < 0.001$ and by NS when non-significant.

P_p decreases with increasing pile size. P_p changes from 0.328 for a pile of 1 corpse to 0.023 for a pile of 200 corpses. The statistical analysis (Prop.test) shows that the P_p for piles of size 1 is significantly different from the other pile sizes (10, 50 and 200 corpses).

The same tendency is observed at 30°C. P_p changes from 0.079 to 0.010 (pile sizes 1 and 200 corpses respectively). Significant differences (Prop.test) are observed between sizes of 1 and 10 corpses, 1 and 200 corpses, 10 and 50 corpses and 50 and 200 corpses.

Comparing P_p between 16°C and 30°C shows higher picking up probabilities at 16°C than at 30°C. These differences are significant (Prop.test) between 16°C and 30°C for sizes of 1 corpse and 10 corpses.

Figure 6b shows the dropping probabilities as a function of pile size and temperature. At 16°C, the dropping probability P_d has a tendency to increase with increasing pile size. P_d changes from 0.043 for piles of size 1 to 0.263 for piles of 200 corpses. Only the difference between piles of size 1 and 50 corpses is significant (Prop.test).

At 30°C, we observe the same tendency. P_d changes from 0.196 to 0.453 (pile sizes 1 and 200 corpses respectively). Two significant differences (Prop.test) are observed: between piles of size 1 and 50 corpses, and between piles of size 1 and 200 corpses.

Comparing P_d between both temperatures shows higher dropping probabilities at 30°C compared to 16°C. The differences are significant (Prop.test) for piles of 10 and 50 corpses.

In summary the picking up probability decreases and the dropping probability increases with increasing pile size for both temperatures. Both tendencies are stronger for 30°C than for 16°C, leading to a higher local amplification of pile formation at 30°C.

Discussion

The first set of experiments has shown that *M. sancta* displacement is significantly modified by temperature. Ant running speed increases with temperature. The detected positive correlation between running speed and temperature has already been found for the desert ant *Ocymyrmex barbiger* (Marsh, 1985), for three *Pogonomyrmex* species (Morehead and Donald, 1998) and for *Dorymyrmex goetschi* (Torres-Contreras and Vásquez, 2004). Temperature has also been shown to influence movement related activities such as foraging (e.g. Gamboa, 1975, 1976; Fowler and Robinson, 1979; Crist and MacMahon, 1991; Human et al., 1998; Ruano et al., 2000), nest entrance activity (Lopez et al., 1992) or outdoor activity (Wehner, 1992; Ruano et al., 2000). To our knowledge no study has tried yet to quantify the dispersal of individual ants in relation to temperature. Here we show that temperature also influences the geometry of ant trajectories: the anisotropy coefficient and the mean free path are negatively and positively (respectively) correlated with temperature. This means that, at high temperature, ants have a tendency to increase the lengths of their straight moves, and when they turn to increase their average turning angle. The net effect of temperature on animal dispersal can now be assessed with the diffusion coefficient D that combines the speed, the mean free path and the anisotropy coefficient in a single parameter. D increases with temperature, ants thus visit more space within the same period of time at 30°C compared to 16°C. This modulation of the diffusion coefficient by temperature probably has an important impact on cemetery formation. The higher dispersion of ants at 30°C leads to a faster transport of corpses via carrying

ants. This will lead to a faster pile formation initially and then to a stronger "competition" between piles at high temperature, speeding up the aggregation process or leading to the formation of bigger piles.

The second set of experiments addressed directly the individual behaviors involved in the corpse aggregation process (picking up and dropping corpses). The probability to pick up a corpse from a pile is negatively correlated with pile size. On the other hand, there is at both temperatures a positive relationship between the size of the pile and the probability to drop a corpse on this pile. Together this represents a local amplification of pile formation, the same that was already found by Theraulaz et al. (2002). Note however that there is a difference between the two studies. In Theraulaz et al. (2002) corpses were initially distributed along arena walls. Due to their thigmotactic tendency, ants aggregated corpses along the arena walls leading to a one dimensional corpse aggregation process. Arena walls are known to stimulate spontaneous dropping (Chrétien, 1996) and they probably also modify picking up and dropping probabilities on piles. In our study, the corpses were dispersed randomly in the entire arena and piles formed everywhere. We thus observed a two dimensional process. Nevertheless, the same local amplification is found in both cases. Moreover, these results are comparable to other studies on piling and sorting behaviors. Franks and Sendova-Franks (1992) have shown that the aggregation processes in brood sorting in ants are based on this kind of mechanisms. In leaf cutting ants, Hart and Ratnieks (2000) have found the same relationship between the number of leaf pieces in a cache and the probability for foragers to deposit a leaf in the cache. Our results also show that temperature modulates the two behaviors involved in this local amplification: the probability to drop is always higher at 30 °C than at 16 °C whatever the pile size, and the probability to pick up is always lower at 30 °C than at 16 °C (even if these differences are not always significant). Therefore, the local amplification will be stronger at 30 °C than at 16 °C: small piles will survive longer at 30 °C and delay the formation of big piles. However, the faster transport of corpses mentioned above will increase the number of contacts between carrying ants and piles, thus it will rather increase the "competition" between piles. The net outcome of the modulation of displacement, picking up and dropping behaviors is difficult to assess and will require further work. In particular the effect of displacement in group on the geometry of individual trajectories (Fourcassié et al., 2003) will require some attention. Overall, this study shows clearly that the amplification process in corpse aggregation, as well as the transport of corpses by carrying ants, is modified by temperature.

Aggregation phenomena are widespread in social insects and, whatever the objects being aggregated, they are often based on similar amplification processes (Franks and Sendova-Franks, 1992; Hart and Ratnieks, 2000; Depickère et al., 2004). Their modulation by an environmental factor (as in corpse aggregation) probably occurs in a lot of aggregation phenomena like mud or twigs aggregation in nest building, collection of pieces of leaves, the storing of seeds or the sorting of brood. In particular, this modulation might be a key to understand how social insects adapt the architecture of their complex nest to a changing environment. Indeed, ants are known to modify their nest architecture in response to environmental variations and internal gradients (temperature, humidity or gas, see Kleineidam and Roces, 2000) to keep good living conditions. They can modify both the external shape (Horstmann and Schmid, 1986; Frouz, 2000) and the internal shape of their nests (Brian, 1983; Kleineidam et al., 2001; Buhl et al., 2004) in order to regulate nest temperature and to ensure its ventilation. They can also modify the internal nest organization, e.g. where they aggregate brood (Ceusters, 1986; Roces and Núñez, 1995; Roces and Kleineidam, 2000; Bollazzi and Roces, 2002). Temperature appears to be one of the key stimuli involved in these processes (Lüscher, 1961; Weber 1972; Hölldobler and Wilson, 1990; Kleineidam et al., 2001). The effects of temperature on movement and corpse aggregation behaviors detected in this study could lead to the existence of aggregation zone preferences by stronger amplification in a particular temperature zone in the nest. This could be a general mechanism to explain how ants choose adequate environmental conditions to ensure a good level of food conservation or larvae growth. However, the overall impact of an environmental factor on aggregation dynamics is difficult to assess from the individual behaviors alone and will require detailed further work at the collective level.

In conclusion, this study shows the sensitivity of individual displacements and aggregation behaviors to temperature in the case of cemetery dynamics in *M. sancta* ants. This work is the first step in our investigation aiming at understanding the influence of environmental factors on aggregation mechanisms and the dynamics of structure formation in ants. The key result is the experimental demonstration that an environmental factor like temperature influences at the individual level the amplification involved in pile formation (by modulating the picking up and dropping behaviors and ant dispersal). This modulation of individual behaviors might play an important role in the establishment of coordination mechanisms between individuals in order to modify the collective structure according to the environmental conditions.

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