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# THE ORGANIZATION OF SOIL DISPOSAL BY ANTS

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Running headline:
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# ABSTRACT

Colonies of *Pheidole ambigua* ants excavate soil and drop it outside the nest entrance. The deposition of thousands of loads leads to the formation of regular ring-shaped piles. How is this pattern generated? This study investigated soil pile formation on level and sloping surfaces, both empirically and using an agent-based model. We found that ants drop soil preferentially in the direction in which the slope is least steeply uphill from the nest entrance, both when adding to an existing pile, and when starting a new pile. Ants respond to cues from local slope to choose downhill directions. Ants walking on a slope increase the frequency and magnitude of changes in direction, and more of these changes of direction take them downhill than uphill. We found that ants carrying soil on a slope wait longer before dropping their soil compared to ants on a level plane. These mechanisms combine to focus soil dropping in the downhill direction, without the necessity of a direct relationship between slope and probability of dropping soil. These empirically determined rules are used to simulate soil disposal. The slight preference for turning downhill we had measured empirically was shown in the model to be sufficient to generate biologically realistic patterns of soil dumping when combined with memory of the direction of previous trips. From simple rules governing individual behaviour an overall pattern emerges, which is appropriate to the environment, and allows a rapid response to changes.

Keywords: **excavation, insect behaviour, organization of work, pattern formation, *Pheidole*, self-organization, waste-disposal**

Dynamic unpredictable environments pose great challenges to the organisms inhabiting them. Behaviours which are appropriate in one situation may become inappropriate when conditions change. Social insects provide many examples of behaviours which are modified to meet environmental changes, from foraging patterns in ants (Sendova-Franks and Franks 1993; Detrain et al. 2001) to brood care in honey-bees (Schmickl and Crailsheim 2002). The self-organized behaviour of many social insects means that the colony's response to the changing environment is often based on changes in the behaviour of individual workers in response to local cues and interactions (Bonabeau et al. 1998; Johnson et al. 2003; Théraulaz et al. 2002). In particular, a single set of local behavioural rules (followed by workers individually) can lead to differing global results depending on environmental conditions (Bonabeau et al. 1998).

Ants are the dominant soil-dwelling insects in many ecosystems (Hölldobler and Wilson 1990). The construction of underground nest chambers leads to the problem of what to do with the displaced soil. This task may be far from trivial: 20g of harvester ants can excavate 20kg of sand in just four to five days (Tschinkel 2004). The excavated soil is deposited on the surface in a wide variety of patterns – circles, crescents or ramps – that can be steep-sided or flat, symmetrical or asymmetrical. Theoretically, in a completely stable environment, the ants could optimize the disposal of a certain volume of soil by building a pile to a predetermined 'optimal' blueprint. For many species however, the environment is unpredictable and dynamic. Part of the soil pile may be crushed by a falling twig or passing animal. A sudden rain storm may wash previously excavated soil back into the entrance hole or even change the incline of the slope on which the soil pile is being built. Changes in humidity may affect the cohesiveness and therefore the angle of repose of the soil, so the ideal angle of the soil pile slope may vary during pile construction (Théraulaz et al. 2003). The strategy used by the ants must be effective in these variable situations. The Brazilian ant *Pheidole ambigua* nests in just such an unpredictable environment, yet colonies create remarkably regular circular soil piles under a range of conditions.

Using biologically determined rules and parameters, we modelled the organization of soil dumping. We used an agent-based modelling approach to reflect the 'bottom-up' organization of ant colonies, by modelling the ants and their interactions at the individual rather than group level. This agent-based model investigates how simple rules, followed by individual ants carrying soil excavated from the nest, lead to the soil becoming organized in particular patterns around the nest entrance. Using the model we also investigate the effect of a hypothetical parameter, memory of the direction of previous trips, on the disposal of soil.

Empirical experiments were carried out to investigate the rules used by the ants to determine their route from the nest and the point at which soil is dropped. We tested whether ants preferentially drop soil in the direction in which the slope is least steeply uphill from the nest entrance (Tofilski and Ratnieks 2005) and investigated the mechanism by which the ants choose the less steeply uphill slope, by testing the hypothesis that the ants are using local cues. The 'local-cues hypothesis' is that ants carrying soil alter their routes as they walk, and specifically that they have a tendency to turn in a downhill direction. The alternative hypothesis is that on leaving the nest entrance the ants scan the horizon from the nest entrance and choose the direction of the lowest horizon, and are not thereafter affected by cues from the local environment. We also investigated whether the ants preferentially drop the soil at or over the top of the soil pile (Tofilski and Ratnieks 2005), or whether probability of dropping soil is based on distance from the nest via an internal template. We incorporated what we learnt from these experiments into the agent-based model.

# METHODS: EMPIRICAL EXPERIMENTS

### Study Species

Ten colonies of *Pheidole ambigua* (Wilson 2003) were found in an area of bare sandy soil, 12m x 12m, at the Fazenda Aretuzina, a farm near São Simão, São Paulo State, Brazil, January to February 2005 and 2006. Colonies nested underground, with a single nest entrance surrounded by a ring of excavated soil, 23-72mm in diameter at the widest point. These soil piles were approximately sinusoidal in cross-section (see Supplementary Fig. 1). For three nests, we captured 10 successive ants exiting the nest hole carrying soil. Their soil particles had a diameter of 1.20± 0.30mm, $N$=10 and the ants had a body length of 3.60± 0.30mm, $N$=10, both measured to the nearest 0.05mm using micrometer callipers. These were all minor workers. *Pheidole* ants have major workers characterized by very large heads but these were seen only rarely and were never observed to carry soil.

### Experiment 1: Adding soil to an existing pile

This experiment tested the ‘slope hypothesis’ that ants choose direction based on slope, by experimentally altering the plane of incline of already established soil piles. If this hypothesis is correct for *P. ambigua*, then when the plane on which dumping occurred was tilted, more ants should choose to drop their soil in the downhill direction. This experiment also allowed us to observe the pattern of soil dropping in relation to the local gradient. For six colonies chosen at random, we carefully removed the soil pile and put the soil aside. We placed a wooden platform 16cm x 22cm with a hole (Ø 10mm) in the centre 30mm above the nest entrance (Supplementary Fig. 2). The orientation of the platform was randomized. A 30mm length of vertical plastic tubing (external Ø 10mm; internal Ø 8mm) linked the nest entrance and the platform. We then placed the soil we had put aside round the tube in a ring. A rectangular piece of cardboard with a cut away section was then rotated around the nest entrance to give a pile with a uniform sinusoidal cross-section of dimensions: height=5mm, width=16mm (see Supplementary Fig. 1). After this manipulation, which took approximately two min to perform, ants carrying soil out of the nest entrance had to continue up the tube and onto the platform to drop their soil. Ants started doing this within seconds of the tube being in place. Soil dumping was video recorded from 80cm vertically above the platform centre for 15 min as a control (Phase 1, Control A). We then dropped one side of the platform 30mm so that the platform was at an angle of 15° from horizontal. The camera was moved 21cm horizontally and angled 15° from vertical to maintain a perpendicular view of the soil pile. Activity was filmed for 30 min in this position (Phase 2, Tilt A). We then angled the platform 15° in the opposite direction and moved the camera to film from the other side for 30 min (Phase 2, Tilt B). Finally we restored the platform to horizontal and the camera to vertical for a further 15 min to control for effects of changing the platform angle (Phase 4, Control B). The artificial piles were stable at these angles, as no collapses or landslides occurred. The workers did not disturb the piles as they walked on them.

A scale bar was placed next to the soil piles to be visible in the video images, for calibration during analysis. Analysis was carried out using Videopoint software (Videopoint 2.5.0 PASCO Scientific, Roseville, California, USA, © 2001 Mark Luetzelschwab and Priscilla Laws) to record the locations in which the ants dropped their loads during the trials. For analysis, we used two pieces of data per soil item: distance from the nest entrance at which it was dropped, and direction relative to the nest entrance in which it was dropped. For the latter the environment was split into two directions, Direction 1 was everything uphill of the nest entrance in Tilt A, and everything downhill in Tilt B. Distance data were used to calculate the local gradient from the known shape of the soil pile. Data were taken from up to 50 soil-dumping ants per phase in Phases 1 & 4 (level) and up to 100 ants per phase in Phases 2 & 3 (tilted). The repeatability of such Videopoint data was tested blind for four clips of video totalling 10 min. The two sets of data were significantly correlated (Pearson's correlation: distance from nest $R=0.93$, $N=10$, $P<0.0001$; angle from nest $R=0.93$, $N=10$, $P<0.0001$).

### Experiment 2: Building a new soil pile

This experiment tested the 'slope hypothesis' as for experiment 1, but in the context of the formation of a new soil pile. This experiment also tested the 'local-cues hypothesis'.

We studied three colonies which had not been used previously. The method was the same as for experiment 1, except that we did not replace the soil pile on the wooden platform, so that ants began dumping on a flat surface. Each trial consisted of one control period with a level platform and two periods with the platform tilted 15°. We placed a circle of paper (diameter 90mm) on the platform, marked with divisions by angle (every 15°) and distance (every 5mm) to aid video analysis. Each period was video recorded until 50 ants had dropped soil. We then swept the platform clean before the next period of recording to prevent the previously dropped soil affecting later dumping. We analysed the trials using Videopoint as in experiment 1. In addition, we quantified the straightness of each ant's path by counting the number of segment lines crossed in each direction for every 5mm the ant moved away from the nest tube until it dropped its soil. To do this, the video was observed in iMovie (iMovie HD v5.0.2(111) ©1999-2005 Apple Computer Inc., Cupertino, California, USA). General Linear Mixed Models (GLMM) and Rayleigh tests (Fisher 1995) were performed using R (R version 2.3.1. Language and Environment © 2006 The R Development Core Team); General Linear Models (GLM) were performed using Minitab (Minitab Statistical Software, © 2000 Minitab Inc, Pennsylvania, USA). Estimates given in results section are mean ± SD.

# METHODS: MODEL

In the model, simulated ants (agents) carrying a piece of excavated soil must leave the nest, walk for some distance in some direction, then drop their soil load and return to the nest. This agent-based model is based on the X-machine system (Holcombe 1988; Eilenberg 1974) in which agents have an individual memory. Each agent has five memory variables: a unique identifier for each agent, whether the agent is carrying soil, the position of the agent within the environment ($\mathbf{r}$,$\boldsymbol{\theta}$), the direction in which agent is heading ($\boldsymbol{\theta}$+/- any change in heading) and a memory of the direction ($\boldsymbol{\theta}$) in which agent most recently dropped soil. All agents are assumed to walk at the same speed and never return to the nest still carrying their soil.

In the model time and 3D space are discretized. The environment is specified using polar coordinates divided into cells ($\mathbf{r}$=1:100, $\boldsymbol{\theta}$=1:100) with the nest entrance (radius 3mm) at the origin. Each cell also has a height dimension, **h**, which allows the surface to grow upwards when soil is dropped. It also allows initial environments to be specified in which the surface is not level. Time is split into time-steps, defined as the time taken for an agent to travel from its current cell to the next cell. Soil dropping is considered to be so quick as to be instantaneous. In the course of a time-step, each agent in turn responds to its environment and undergoes one of the six processes outlined in Fig. 1. Initially agents have no soil and are in the nest: $\mathbf{r}_0$=0, $\boldsymbol{\theta}_0$=0. Their initial direction of heading is determined randomly or by memory of previous location. When the agents move, they first use their position and direction of heading to detect the local slopes from their own position to the cell ahead and to ahead right and ahead left. Ants have been shown to be able to detect slopes and respond accordingly (Wohlgemuth et al. 2001). The agents may change their direction of heading depending on a function of the slope ahead ($\alpha_{\mathrm{SlopeAhead}}$). If a change in direction is made, the direction and magnitude (**c**) of the change depends the slopes ahead (straight, right and left). The agent then moves one cell in the direction it is now heading and tests whether to drop soil, depending on a function of distance from the nest, $\eta_r$. If the function determines that the agent drops the soil, the soil dropped by an agent is added to the height of the cell which is the agent's current position. As the grid of cells is defined using polar co-ordinates, the area of the cells increases with the radius. The effect of a piece of soil is averaged over the whole cell, i.e. the increase in height is approximated by the diameter of a piece of soil ($\omega$), divided by the area of the cell. Ants return directly to the nest, as has been observed for *Messor barbarus* (Chrétien 1996) and *P. ambigua* (EJHR personal observation). In this model agents do not interact directly with other agents, only indirectly by affecting the environment. The soil dropped during a time-step is stored in a temporary matrix and at the end of the time-step the height of all the cells are updated simultaneously. This gives concurrency to the events within a time-step which is appropriate, as in a biological situation several ants could drop soil at the same time. The constants and parameters used in the model are listed in table 1.

# MODELLING EXPERIMENTS

For the simulation experiments, the model was applied to soil dumping as seen in *P. ambigua*. The model was implemented in MatLab (MatLab Version 6.1.0.450 Release 12.1, © 1984-2001 The MathWorks, Inc, Natick, Massachusetts, USA). Statistical tests were carried out using R and Minitab.

## Role of Memory

Simulations of soil dumping were carried out over a range of environments: level flat ground, sloping flat ground, adding to a ring-shaped pile, and adding to a ring on a slope (supplementary table 1). Each trial corresponded to six hours of soil dumping (86400 time-steps) and trials were replicated 10 times. Memory was investigated at two extremes. In no memory simulations, subsequent behaviour was independent of previous behaviour. In simulations with memory, agents always started out from the nest heading in the direction in which they previously dropped their soil. The agent's memory was updated to the new direction in which soil was dropped each time a drop was made. This memory was assumed to remain constant between drops. We also ran the simulation to match the procedure in empirical experiment 1 with 15 min of empirical data represented by 3600 time-steps, and analysed the data using the same GLMM which we had applied to the empirical data.

## Response to Gradient

Preference for turning downhill was investigated at three levels: no preference for the downhill direction ($\mathbf{b}_{\text{downhill}}$=0.5), empirically observed probability of choosing downhill

($\mathbf{b}_{\text{downhill}}$=0.58) and deterministic choice of the downhill direction ($\mathbf{b}_{\text{downhill}}$=1). This was investigated with and without memory. These simulations were carried out on a flat sloping environment and were run for a longer period of time, corresponding to 12 days assuming soil is excavated for 12 hours per day (2,073,600 time-steps). Due to the length of time these longer simulations took to run, each was replicated just five times.

# RESULTS: EMPIRICAL EXPERIMENTS

**Experiment 1: Adding soil to an existing pile**

The results supported the 'slope hypothesis', for the first tilted phase, as significantly more ants dropped their soil in the downhill direction: Tilt A ($t_{1363}$=3.6, $P<0.001$) (Fig. 2a) (GLMM with colony and phase as fixed effects, colony as a random effect and a binomial error structure). A difference between the proportions dropping soil in each direction was also seen in the first control period Control A (GLMM: $t_{1363}$=4.6, $P<0.001$). However, Tilt A was significant in the opposite direction to Control A, showing that a switch in preferred direction of dumping had occurred (GLMM post-hoc comparison: $P<0.05$) (Fig. 2a) When the substrate was tilted in the opposite direction (Tilt B) again a significant change in the proportions dumping in each direction occurred (GLMM post-hoc comparison: $P<0.05$), although there was no significant difference between the numbers dumping in each of the two directions. When the platform was returned to level (Control B), no significant change occurred, and there was no significant difference between the numbers dumping in each of the two directions. Colony also had a significant effect on numbers dropping soil in each direction (GLMM: $t_4=3.2$, $P<0.05$).

During the level (control) periods, more ants dropped their soil on the outer slope of the pile (23.3± 14.6%) than the inner uphill slope (4.9± 4.6%), though this difference was not statistically significant (Wilcoxon signed rank test: $W=15$, $N=6$, $P=0.06$). The majority (70.7± 19.5%) of the ants dropped their soil beyond the artificial soil pile on the level surface (Supplementary Fig. 4). Similar assessments was not carried out on the tilted phases, due to the confounding effect of the overall slope on the routes of the ants. Ants left the nest carrying soil at a rate of 0.27± 0.1ants/sec.

## Experiment 2: Building a new soil pile

When ants are building a new soil pile, the results support the 'slope hypothesis'. Although the GLMM gives no significant difference in the proportions dumping in each direction between the control and the first tilted phase (Fig. 2b) (GLMM post-hoc comparison (Bretz et al. 2001): parameter estimate=-3.5, 95%CI lower=-5.51; upper=-1.54) because the control was already biased in the direction which became downhill (Rayleigh test of uniformity: *Rbar*=20, $P<0.001$), on the slope (Tilt 1) significantly more ants drop their soil downhill than uphill (Fig. 2b) (GLMM: $t_{443}=2.6$, $P<0.01$) which is not the case for the control (GLMM: $t_{443}=0.73$, $P<0.01$). When the substrate is tilted in the opposite direction, a significant switch occurs (GLMM post hoc comparison: $P<0.05$)

with the final distribution of soil dumping biased in the direction which is now downhill (Rayleigh test of uniformity: *Rbar*=19, $P<0.001$).

When dumping soil on a level platform, the number of segments through which the ants travel to the right or left while they travel one ring outwards follow a Poisson distribution of mean 0.35 ($\chi^2_2=0.41$, $P=0.81$). This indicates that an ant's probability of turning a certain number of segments is independent of the number of segments it has previously turned. 38% of ants changed their course by at least one segment; 99% of turns observed were less than 45°. Using the net direction of turns by each ant over its whole outward journey, there was no significant difference between the number which made a net turn to the right versus the left (chi-square test: $\chi^2_1=3.3$, $N=89$, $P=0.07$).

In contrast on a 15° slope the distribution of turns does not follow a Poisson distribution ($\chi^2_2=214.0$, $N=1355$, $P<0.001$). The difference is due to fewer than expected ants making no turn, and more ants than expected making at least one turn. On the slope significantly more ants make a net downhill turn (58.6%) than a net uphill turn (41.4%) ($\chi^2_1=5.0$, $N=169$, $P<0.05$).

The first 12 ants to drop soil on the new paper from each trial were analyzed to see if the angle from the nest at which an ant dropped its soil was correlated with the angle from the nest of the previous ant. No correlations were found (Pearson's correlation $N=11$: Trial 1: $R=-0.31$, $P=0.35$; Trial 2: $R=0.32$, $P=0.35$; Trial 3 $R=-0.01$, $P=0.99$).

Colony had no effect on the mean distance at which soil was dropped (GLM with colony and phase as fixed effects, colony as a random effect: $F_{2,447}$= 2.3, $P$=0.1) so for analysis of the probability distributions the data were pooled across colonies. The probability of soil dropping on the level is related to distance from the nest by a logistic function ($r^2$=0.99) (Fig. 3a). The distances at which soil was dropped during the tilted phases does not fit this logistic function (chi-square test: $\chi^2_{21}$=72, $P$ <0.001), because during the two tilted phases, the mean distance at which soil is dropped is significantly greater (Tilt A, 30.48± 15.51mm; Tilt B, 29.46± 13.79mm) than when on the level (26.55± 15.43mm) (ANOVA: $F_{2,447}$=7.38, $P$<0.001). The mean distance at which soil was dropped did not differ between the three directions uphill, downhill and level (Supplementary Fig. 3) either when flat or during either tilted phase (ANOVA: $F_{4,445}$=0.98, $P$=0.41). The distances at which soil was dropped on a slope fits to a logistic function ($r^2$=0.99) but with different parameters (Fig. 3b). The distribution of distances at which soil is dropped during the control phases of Experiment 1 fits to the same logistic function which was fitted to the tilted phases of Experiment 2 (chi-square test: $\chi^2_{22}$=20, $P$=0.58). These distributions were used in the parameter $\boldsymbol{\eta}_\mathbf{r}$ in the model.

For each trial the mean speed of the first 20 outward-bound soil-carryings ants was calculated over their journey from the central tube to where they dropped their soil. No differences in mean speed were seen between trials (ANOVA: $F_{3,56}$=0.58, $P$=0.63) giving an overall walking speed of 3.8± 2.1mms$^{-1}$, $N$=60.

# MODELLING EXPERIMENTS: RESULTS

## Role of Memory

When the agents did not use memory of previous trips, on a level flat surface, soil was dropped symmetrically (Rayleigh test of uniformity: *Rbar*= -77, *P*=0.99). When the initial environment was sloped by 15° there was no bias towards more soil dumping in the downhill direction (Rayleigh test of uniformity: *Rbar*= -155, *P*=0.99). This contrasts with the empirical results, where there was a significant bias downhill. Adding soil to an existing symmetric ring-shaped pile was simulated across conditions based on empirical experiment 1. The pattern of soil dropping (Fig. 2c) did not match the experimental results (see Fig. 2a) when the model was run with no memory. There were no significant differences between the proportions of agents dumping soil in each direction at any phase of the experiment (GLMM C1: $t_{9457}$=1.1, *P*=0.27; T1: $t_{9457}$=0.73, *P*=0.47; T2: $\mathrm{t}_{9457}$=0.36, *P*=0.72; C2: $t_{9457}$=0.078, *P*=0.94).

When memory was used by the agents in choosing direction to leave the nest, soil was not dropped symmetrically, even on a level flat surface (Rayleigh test of uniformity: *Rbar*= 48, *P*<0.001). This is also what was seen in experiment 2, but differs from the results when no memory was used. The distribution across the radial segments was significantly more variable than in the equivalent simulation without memory (no memory standard deviation 6.0± 0.48mm; with memory standard deviation 10.2± 1.7 mm, two-tailed *t*-test: $t_{18}=7.43$, $P<0.001$) showing that the soil was dropped in a more clumped distribution when memory was used. When this flat surface was sloped there was a bias for soil dumping in the downhill direction (Rayleigh test of uniformity: *Rbar*= 42, $P<0.001$).

When the simulation of agents adding soil to an existing pile was repeated with memory (Fig. 2d), the results were qualitatively similar to the empirical biological results (Fig. 2a). When the environment was tilted, significantly more agents dropped soil in the downhill direction than uphill (GLMM T1: $t_{9452}=2.85$, $P<0.01$) which was also the case in the empirical results. However in the model, when the environment was tilted in the opposite direction, the agents were able to switch to dropping more in the new downhill direction (GLMM T2: $t_{9452}=4.39$, $P<0.001$), whereas in the experiment the switch was not significant. In the biological data, there was a significant difference between the numbers dumping in the two directions in the first control phase, though not the second. In the model with memory there was also a significant difference in one of the controls (GLMM C1: $t_{9457}=1.31$, $P=0.19$; C2: $t_{9457}=2.23$, $P<0.05$). The model results included more agents for the same period of time than the experimental results, as during the biological experiment no more than 50 ants were recorded during a control phase and no more than 100 during a tilted phase, and the colonies were variable in their flow.

## Response to Gradient

The experimentally observed proportion of turns which were in the downhill direction was just 58%. Although this was statistically greater than the random expectation, it is only a slight preference. This simulation experiment aimed to investigate whether this preference (**b**=0.58) is great enough to have an effect on the pattern of soil dumping, with and without memory, compared to **b**=0.5 (random choice) and **b**=1 (always choose downhill) (Fig. 4). A General Linear Model was used to compare the heights added to the segments perpendicularly uphill and perpendicularly downhill over the different levels of memory and preference for turning downhill, and a highly significant effect was found for memory (GLM: $F_{1,58}$=1947, $P<0.001$), **b** (GLM: $F_{2,57}$=2331, $P<0.001$) and the interaction between memory and preference for downhill (GLM: $F_{2,57}$=2081, $P<0.001$).

With no memory of previous direction, at the experimentally observed probability of turning downhill (**b**=0.58) (Fig. 4c) there was no significant difference in the heights added to the most uphill segment and the most downhill (Tukey HSD: $t$=0.74, $P$=0.99) showing that the agents were not dropping significantly more soil downhill. This pattern of soil dropping with **b**=0.58 does not differ significantly from the pattern formed when no preference for turning downhill is used (Fig. 4a), either for the height added uphill (Tukey HSD: $t$=0.18, $P$=0.99) or downhill (Tukey HSD: $t$=0.35, $P$=0.99). However, when **b**=1 (Fig. 4e), significantly more soil is dropped in the downhill direction than uphill (Tukey HSD: $t$=4.73, $P<0.01$).

When the agents act on the memory of the previous direction in which they dropped soil the results are dramatically different. In the case of the experimentally observed probability of turning downhill (**b**=0.58) (Fig. 4d) significantly more soil is added in the downhill than uphill direction (Tukey HSD: $t$=30.5, $P$<0.001). As can been seen from Fig. 4d, the agents have filled up the downhill direction until it is level with the nest entrance. This is significantly different from the pattern seen when there is no preference for downhill (**b**=0.5) (Fig. 4b), both for uphill (Tukey HSD: $t$=10.3, $P$<0.001) and downhill (Tukey HSD: $t$=23.3, $P$<0.001). When **b**=1, an unexpected pattern emerges (Fig. 4f). Not only do the agents drop more soil downhill than uphill (Tukey HSD: $t$=176.4, $P$<0.001), but they continue dropping soil in that direction, even though the downhill pile is more than twice as high as the uphill one.

# DISCUSSION: EMPIRICAL EXPERIMENTS

The empirical data support the ‘slope hypothesis’ of Tofilski and Ratnieks (2005) that ants choose the less uphill slope. In both experiment 1 and experiment 2 when the substrate is tilted, more of the ants walk down the slope to drop their soil, as opposed to up the slope. This is beneficial for the colony because the soil is less likely to roll back towards the nest if carried downhill. There may also be advantages in terms of energy efficiency in walking down rather than up a slope while carrying a load. However, in experiment 1 when the substrate was tilted in the opposite direction, the ants did not make a complete switch to the new downhill direction in the 30 min they were given. Ants may be showing route fidelity to the previous direction of dumping (Wehner 1970), if relatively few ants are involved in dumping, and they do not immediately respond to changes in the environment. If so, the data suggest that ants may have more route fidelity to previously downhill directions, than to previously flat ones. Alternatively, the successive changes in the plane of incline of the dumping platform may have affected dumping. Colony also had a significant effect on direction of soil dumping, suggesting that some colonies have a bias in a particular direction. Our experiments were performed in the context of natural nest entrances, so cues from the sun and landmarks such as trees were available to the ants, and may be responsible for this bias, or there could be an effect from the angle of the subterranean tunnels before the ants entered the vertical tube.

The analysis of the routes taken by loaded ants during a trip from the nest entrance to where they finally drop their soil supported the 'local-cues hypothesis' that the ants respond to local differences in slope and adjust their direction accordingly. In experiment 2 there was no significant bias to the left or right while ants carried soil out from the nest on the level, and the final angles at which soil was dropped followed a uniform distribution. It is therefore reasonable to assume that the initial angles at which the ants leave the nest are also randomly distributed at the colony level, although individuals may have fidelity to a particular angle. Almost all turns made by ants are small deviations from their path (<45°). Avoiding large turns would reduce the total distance covered by the ants, and prevent them returning to the nest with their load. The data indicate that each turn is independent of the last, and that there is a constant probability of turning by a certain amount. In contrast the results on a sloping substrate show that on a slope more turns occur, and that these turns are significantly more often downhill than uphill. The final distribution of soil dumped on a slope is biased in the downhill direction. We did not find any effect of the route of the previous ant on the subsequent one, suggesting that ants were neither following pheromone trails nor visually following the ant in front. The data on the route of the ants suggest a mechanism for the preference for the downhill direction. Ants are responding to the local environment and changing their routes as they walk away from the nest either by directly detecting local slope (Wohlgemuth et al. 2001) or by assessing a narrow range of horizon ahead of them. The data do not support the alternative hypothesis that ants scan the horizon on leaving the nest and make an initial choice of direction which they then maintain. However, ants may still make some initial choice based either on the horizon or previous memory, and then make further course corrections during the trip.

Previous work on ant soil disposal suggests that ants should drop soil at or over the top of the soil pile (Tofilski and Ratnieks 2005). We found no conclusive evidence that *P. ambigua* follow this rule. While many ants did drop soil on or just over the summit in experiment 1, others dropped their soil on before the summit or on the flat area beyond the pile. When on a slope (uphill or downhill) in experiment 2, ants tended to walk further before dropping their soil compared to when on level ground. Interestingly, the ants from experiment 1 (dumping soil on an existing soil pile) followed the same pattern of soil dropping with distance as did the ants in the tilted phase of experiment 2. This suggests that walking on a slope, whether caused by an existing soil pile or by the underlying substrate, causes the ants to wait longer before dropping their soil. This fits in with the observations of (Tofilski and Ratnieks 2005) that *Dorymyrmex* ants dropped their soil closer to the nest on the flattened half of a soil pile than on the half which was left intact. This distance-dependant probability distribution of soil dropping, $\boldsymbol{\eta}_\mathbf{r}$ which was used in the model could be an internal template for the basic form of the soil pile, which is then modified by other rules in response to the local environment. Alternatively this distribution could itself be an emergent property based on environmental cues which were not detected in this study.

# DISCUSSION: MODEL

Memory of directions of previous soil dumping has been shown in the field in *Cataglyphis bicolor* (Wehner 1970) and probably occurs in *Dorymyrmex* sp. (Tofilski and Ratnieks 2005), although *Messor barbarus* shows no directional fidelity in soil dumping (Théraulaz et al. 2003). Individual memory is a component also of the foraging systems of many ant species (Harkness and Maroudas 1985; Traniello 1988; Narendra et al. 2007), so it is quite possible that *P. ambigua* is able to remember the direction from which it returns to the nest, and use that direction again, as our model suggests. When memory was used by the agents in choosing the direction to leave the nest, soil dumping in a level environment was symmetrical overall, but variable around the circle because the random initial distribution of heading angles is not uniform, leading to clumps of soil. When the environment was sloped, the agents were able to adapt to the changed environment by preferentially dumping downhill, as is seen in natural situations. However in the short simulations (Fig. 2d), while the agents did dump more soil in the downhill direction, one of the level controls also showed a significant difference between the two directions. This suggests that over short time periods (15 min in this experiment) the clumping of soil dumping by ants with memory can lead to asymmetries. However, the preference for dumping in the downhill direction would tend to even out these clumps over time, because once the concentration of soil dumping in some areas has caused a significant slope to form, ants would tend to turn down the slopes away from these higher areas, thus filling in the gaps. Over time this would produce a level surface, as seen in the results of the longer simulation (Fig. 4d).

This model shows that there is no necessity for ants to assess the quality of a particular direction, or remember the slope associated with an angle; simply returning to the direction in which the soil was dropped is sufficient, provided course improvements are made during the outward journey. In this model memory is reliable and does not decay with time. It is likely that in real ant systems, there will be error in returning to the same direction, and that this will increase if the delay between trips is high. Some error in self-organized systems can be very important in helping the ants respond to changes in the environment (Deneubourg et al. 1983). In addition the number of ants involved in soil disposal is likely to affect the strength and duration of memory. Although no significant effects in preliminary tests were found across the range 25-100 agents, in a much larger population of soil dumpers where each ant makes fewer trips, the individual memories would be updated to changes in the environment only slowly. In very small populations each individual would make a relatively larger contribution to the overall pattern, so this model would predict an initially clumped pattern of soil dumping, as the initial directions taken by the few ants would be favoured over other directions. However, in a small population, the memories would be rapidly updated as each ant would make many trips, so as the soil pile built up, the ants would change their directions and even out the pile.

The modelling results clearly show that the experimentally observed preference for turning downhill (58%) is enough to have a significant impact on the soil dumping pattern, provided the ants remember their previous direction of dumping. If they remember this direction, then with a probability of turning downhill of 0.58, they drop more soil downhill than uphill, bringing the downhill pile up to the level of the nest entrance. Without memory however, this pattern is not seen, and a preference of 0.58 does not differ in effect from random choice. When the ants are forced to choose the downhill direction whenever it is above their threshold of detection (**b**=1) then in the case without memory, they are able to drop more soil downhill. If they use memory however, they get locked into a suboptimal situation. These ants quickly become concentrated on the downhill direction because all their turns take them downhill and they remember their previous direction, so eventually they build up the pile in the downhill direction above the height of the uphill direction. Because very little soil is dropped in the area immediately around the nest, this area continues to be downhill relative to the nest entrance. This means that the ants continue to choose these directions, even though a global view would show them they would have to climb less if they set out along the level instead of downhill.

In some of the simulations (Fig. 4b,d,e) ‘shoulders’ formed on the sides of the hill. These are in the directions which are effectively on the level relative to the nest entrance. Soil accumulates here because the slope is below the threshold to trigger slope behaviours (higher turning rates) so more agents stay on their original path, and also agents which are uphill of these regions tend to turn downhill and join the agents already in this area. These effects are compounded if memory is used.

Overall, the results suggest a simple system of organization used by *P. ambigua* to dispose of excavated soil, both on the level and on a slope. *P ambigua* drop their soil as a function of the distance they walk from the nest. This basic template is modified in response to the environment, as soil-carrying *P. ambigua* respond to a slope in three ways: increasing the frequency and magnitude of turns, tending to turn downhill, and waiting longer before dropping their soil. The combination of these three factors makes them more likely to drop their soil downhill when on a slope. A further dimension could be provided by memory. If the ants are more likely to start a second dumping trip in the direction from which they returned after dropping their soil on a previous trip, this would lead over time to a concentration of the ants dumping soil in the downhill directions. The model does not fully explain sand disposal behaviour, but does strongly support the idea that these observed rules are sufficient to produce an appropriate pattern of soil dumping in a range of environments, even if the preference for turning downhill is slight, provided the rules are combined with memory of the direction in which the ant has previously dumped soil and a preference for returning to this direction with later loads. Further work studying individually marked ants is required to test this memory hypothesis. The rules we suggest do not require the ants to have global knowledge of the slopes in the environment, or even to scan the horizon for the lowest point (Tofilski and Ratnieks 2005; Franks et al. 2004). From these simple rules governing individual behaviour an overall pattern emerges, which is appropriate to the environment, and quickly adapted to changes.

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# REFERENCES

**Sendova-Franks, A. B. & Franks, N. R.** 1993. Task allocation in ant colonies within variable environments (a study of temporal polyethism: experimental). *Bulletin of Mathematical Biology*, 55, 75-96.

**Detrain, C., Natan, C. & Deneubourg, J. L.** 2001. The influence of the physical environment on the self-organised foraging patterns of ants. *Naturwissenschaften*, 88, 171-174.

**Schmickl, T. & Crailsheim, K.** 2002. How honeybees (*Apis mellifera* L.) change their broodcare behaviour in response to non-foraging conditions and poor pollen conditions. *Behavioral Ecology and Sociobiology*, 51, 415-425.

**Bonabeau, E., Théraulaz, G., Deneubourg, J. L., Franks, N. R., Rafelsberger, O., Joly, J. L. & Blanco, S.** 1998. A model for the emergence of pillars, walls and royal chambers in termite nests. *Philosophical Transactions of the Royal Society of London. B.*, 353, 1561-1576.

**Johnson, C. A., E., L., Allard, D. & Gobin, B.** 2003. The emergence of collective foraging in the arboreal *Gnamptogenys menadensis* (Hymenoptera: Formicidae). *Naturwissenschaften*, 90, 332-336.

**Théraulaz, G., Bonabeau, E., Fourcassié, V., Nicolis, S. C., Sole, R. V., Fernandez, P., Blanco, S., Fournier, R., Joly, J. L., Dalle, P., Grimal, A. & Deneubourg, J.-L.** 2002. Spatial patterns in ant colonies. *Proceedings of the National Academy of Sciences, U.S.A.*, 99, 9645-9649.

**Hölldobler, B. & Wilson, E. O.** 1990. *The Ants*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.

**Tschinkel, W. R.** 2004. The nest architecture of the Florida harvester ant, *Pogonomyrmex badius*. *Journal of Insect Science*, 4, 1-19.

**Théraulaz, G., Gautrais, J., Camazine, S. & Deneubourg, J. L.** 2003. The formation of spatial patterns in social insects: from simple behaviours to complex structures. *Philosophical Transactions of the Royal Society of London Series a-Mathematical Physical and Engineering Sciences*, 361, 1263-1282.

**Tofilski, A. & Ratnieks, F. L. W.** 2005. Sand pile formation in *Dorymyrmex* ants. *Journal of Insect Behavior*, 18, 505-512.

**Wilson, E. O.** 2003. *Pheidole in the New World. A dominant, hyperdiverse ant genus.* Cambridge, Massachusetts: Harvard University Press.

**Fisher, N. I.** 1995. *Statistical Analysis of Circular Data*. Cambridge: Cambridge University Press.

**Holcombe, M.** 1988. X-machines as a basis for dynamic system specification. *Software Engineering Journal*, 3, 69-76.

**Eilenberg, S.** 1974. *Automata, Languages and Machines*. London: Academic Press.

**Wohlgemuth, S., Ronacher, B. & Wehner, R.** 2001. Ant odometry in the third dimension. *Nature*, 411, 795-798.

**Chrétien, L.** 1996. Organisation spatiale du matériel provenant de l'excavation du nid chez *Messor barbarus* et des cadavres d'ouvrières ches *Lasius niger* (Hymenoptera: Formicidae). PhD Thesis, Université Libre de Bruxelles.

**Bretz, F., Genz, A. & Hothorn, L. A.** 2001. On the numerical availability of multiple comparison procedures. *Biometrical Journal*, 43, 645-656.

**Wehner, R.** 1970. Études sur la construction des cratères au-dessus des nids de la fourmi *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insectes Sociaux*, 17, 83-94.

**Harkness, R. D. & Maroudas, N. G.** 1985. Central place foraging by an ant (*Cataglyphis bicolor* Fab) - a model of searching. *Animal Behaviour*, 33, 916-928.

**Traniello, J. F. A.** 1988. Variation in foraging behavior among workers of the fire ant *Formica schaufussi*: ecological correlates of search behavior and the modification of search pattern. In: *Interindividual behavioral variability in social insects* (Ed. by Jeanne, R. L.), pp. 91-112. Boulder, Colorado: Westview Press.

**Narendra, A., Cheng, K. & Wehner, R.** 2007. Acquiring, retaining and integrating memories of the outbound distance in the Australian desert ant *Melophorus bagoti*. *Journal of Experimental Biology*, 210, 570-577.

**Deneubourg, J. L., Pasteels, J. M. & Verhaeghe, J. C.** 1983. Probabilistic behavior in ants - a strategy of errors. *Journal of Theoretical Biology*, 105, 259-271.

**Franks, N. R., Britton, N. F., Sendova-Franks, A. B., Denny, A. J., Soans, E. J., Brown, A. P., Cole, R. E., Havardi, R. J., Griffiths, C. J. & Ellis, S. R.** 2004. Centrifugal waste disposal and the optimization of ant nest craters. *Animal Behaviour*, 67, 965-973.

**Sumpter, D. J. T., Blanchard, G. B. & Broomhead, D. S.** 2001. Ants and agents: a process algebra approach to modelling ant colony behaviour. *Bulletin of Mathematical Biology*, 63, 951-980.

Table 1. The values and derivation of the constants and parameters used in the simulation experiments

| Symbol | Summary | Notes | Value used | Source and comments |
|---|---|---|---|---|
| $\omega$ | Soil particle size | The diameter of a piece of soil carried by an ant | 1mm | Empirically determined |
| $\gamma$ | Slope detection range | The number of cells over which an ant detects slope | 1 cell | Mean length of ant= 3.6mm (empirically determined). At low **r** the diagonal distance to the next cell to the right/left is less than the mean length; at high **r** it is greater than the mean length. 1 cell is assumed to avoid problems with choosing between net slope and total slope, if the ground is uneven. |
| $\tau$ | Time-step duration | Time taken for an ant to traverse a cell | 0.25sec | Mean ant speed= 4mms$^{-1}$ (empirically determined, experiment 2). Radial length of a cell is set to the diameter of a soil particle ($\omega$). A time-step is the time taken for an ant to traverse a cell, *i.e.* 1mm/4mms$^{-1}$ |
| $\varphi$ | Traffic flow rate | The number of ants which leave the | 1 ant per 4 sec | Empirically determined, experiment 1 |

| | | | | |
|---|---|---|---|---|
| | | nest in each time step | (1 ant per 16 $\boldsymbol{\tau}$) | |
| $\boldsymbol{\zeta}$ | Ant number | Total population of ants involved in soil dumping | 50 | Estimate: preliminary experiments show no significant effects on pattern formed over the range $\boldsymbol{\zeta}$= 25-100. |
| $\mathbf{g}$ | Minimum detectable gradient | The gradient above which ants behave as on a slope | 0.08 | This corresponds to a slope of 15°, which it is empirically shown that ants respond to |
| $\mathbf{c}$ | Magnitude of change in heading | The number of cells to the right/left an ant moves | 0-12 cells | From empirical experiment 2; details in supplementary information |
| $\boldsymbol{\alpha}_{\mathbf{c}}$ | Probability of making change in heading of given magnitude | This is affected by local slope | $\alpha_0$=0.27 …<br>$\alpha_{>12}$=0<br>(level)<br>$\alpha_0$=0.21 …<br>$\alpha_{>12}$=0<br>(slope) | 0 cells is the minimum change in heading per step forward; 12 cells the maximum. Probabilities determined from empirical experiment 2; intermediate probabilities and details are in supplementary information |
| $\mathbf{b}_{direc}$ | Probability of change being in particular direction | Right/left, up/downhill | $\mathbf{b}_{right}$=0.5<br>$\mathbf{b}_{left}$=0.5<br>(level)<br>$\mathbf{b}_{down}$ =0.58 | From empirical experiment 2; details in supplementary information. Investigated in simulation experiments |

| | | | | |
|---|---|---|---|---|
| | | | $\mathbf{b}_{up}$=0.42<br>(slope) | |
| $\boldsymbol{\eta}_{\mathbf{r}}$ | Probability of dropping soil at a given distance, **r** | A function the distance from the nest | Logistic function | Determined from fit to empirical data. See supplementary information for details and parameters of equation |

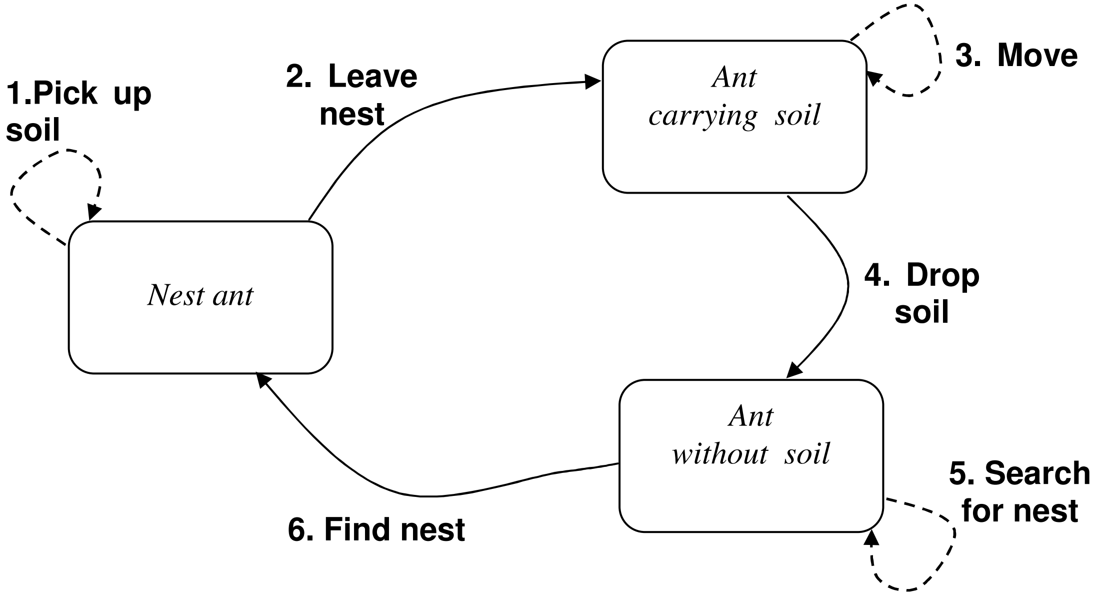


Figure 1. The three general behavioural states are indicated in the boxes. Each state has an action associated with it (---►) and these states are connected by transition actions (—►). 1) Pick up soil: agents pick up soil within the nest at the rate determined by the traffic flow, **φ**. 2) Leave nest: agents which have picked up soil leave the nest in the direction which they are heading. 3) Move: all agents carrying soil outside the nest follow the 'move' rules. 4) Drop soil: The soil dropped by an agent adds to the height of the cell which is the agent's current position, and the agent remembers the angle at which the soil was dropped. 5) Search for nest: all agents outside the nest with no soil return towards the nest, one cell per time-step by a direct route until they find it. 6) Find nest: agents without soil which find the nest enter it and remain 'nest ants' until they pick up soil again and leave.

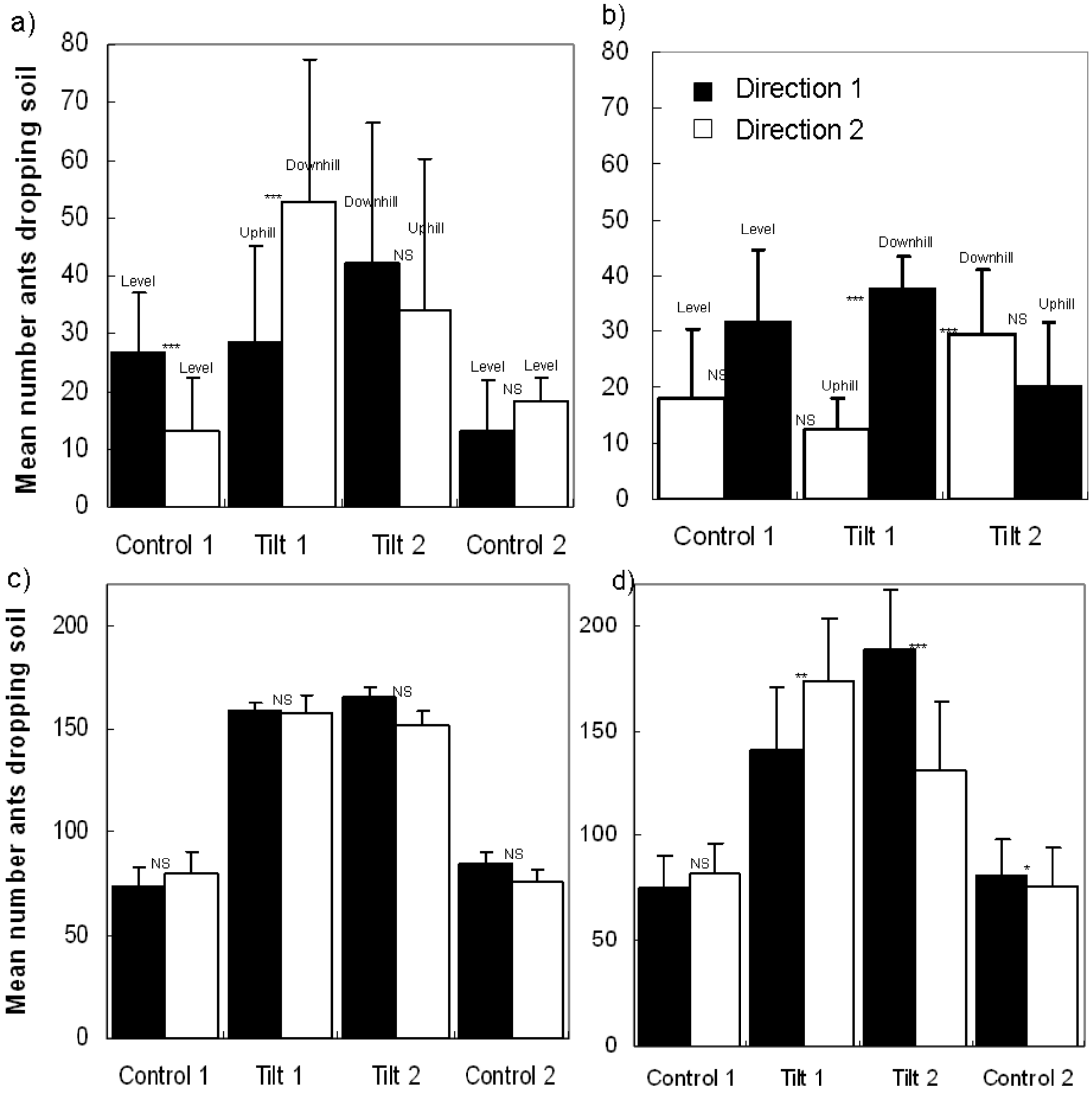


Figure 2. Number of ants dropping soil in each of two directions (mean +SD). a) Experiment 1. *N*=6. Total number of ants for each phase: Control 1=239, Tilt 1=489, Tilt 2=457, Control 2=190. Tilt periods were twice as long as the control periods. b) Experiment 2. *N*=3. Total number of ants was 150 per phase. c&d) Model data without (c) and with (d) memory. *N*=10. ***P<0.001, **P<0.01, *P<0.05, NS indicates P>0.05.

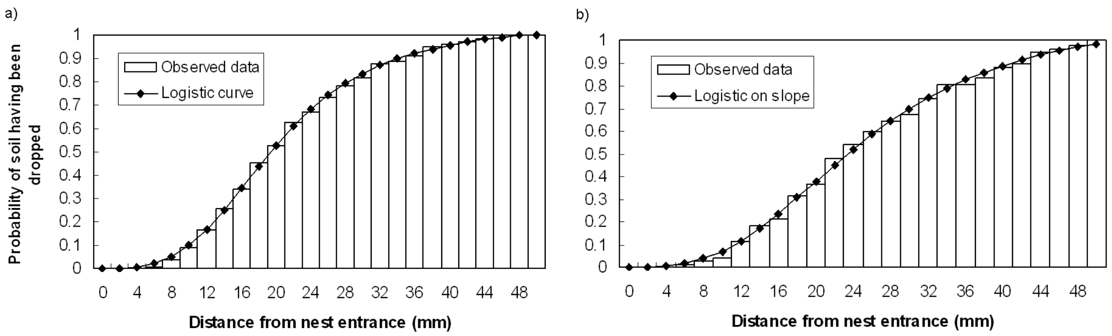


Figure 3. Empirical data on probabilities of soil having been dropped by a given distance from the nest and logistic fits for level (a) and sloping (b) environments.

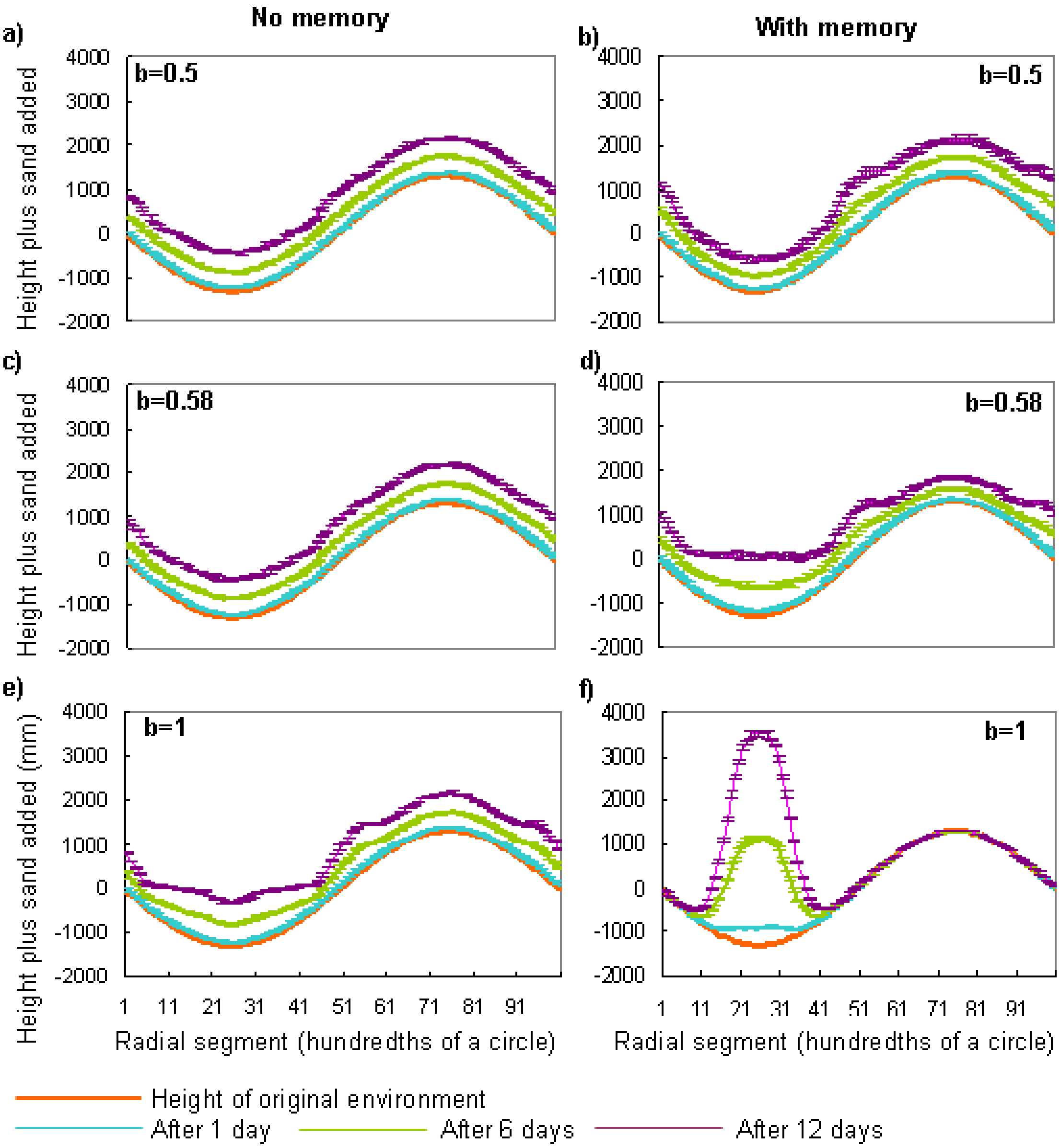


Figure 4. Total height of each radial segment of the environment initially and with soil added. Comparing no memory and with memory against preferences for turning downhill: random (**b**=0.5); experimentally observed probability (**b**=0.58); deterministic (**b**=1). Negative heights are downhill relative to the nest entrance, positive ones uphill. Heights after days are mean± SD, *N*=5.

## Supplementary information

# Details of Agent-based model

This agent-based model is based on the X-machine system. X-machines are similar to finite state machines (FSM) in that agents are autonomous communicating machines with inputs which determine transitions between a finite set of states. X-machines, however, also have memory, so that each agent has a set of variables. These variables, together with inputs from the environment (including other agents), determine the state transitions.

## Agents

Each agent (ant) has the following set of memory variables.

- `ID`: Unique identifier for each ant
- `SOIL`: Whether ant is carrying soil. Soil=1; No soil=0
- `POS`: Position of ant within the environment. (**r**,**θ**)
- `HEAD`: Direction in which ant is heading. (**θ**+/- any change in heading)
- `MEMO`: Direction (**θ**) in which ant most recently dropped soil

## Environment

Each Cell has:

- `ID`: Unique cell identifier (**r**,**θ**)

- `HEIGHT`: Height dimension, (**h**) determined by initial height plus soil dropped (adjusted for cell area)

## Behavioural Processes

### 1. Pick up soil

Initially ants are:

```
ant[ID=n SOIL=0 POS=($\mathbf{r}_0$,$\boldsymbol{\theta}_0$) HEAD=$HEAD_0$ MEMO]
```

$HEAD_0$ is determined randomly or by memory of previous location, depending on the memory parameter, **μ**:

```
If $\boldsymbol{\mu}$ =0
    $HEAD_0$ = rand(1:100)
Else if $\boldsymbol{\mu}$ =1
    $HEAD_0$ = MEMO
End
```

Ants pick up soil within the nest at the rate determined by the traffic flow. **φ** ants per iteration are randomly chosen from the nest population to pick up soil. Where **φ <**1, one ant per 1/ **φ** iterations is randomly chosen from the nest population to pick up soil.

```
$ant_t$[SOIL=0] → $ant_{t+1}$[SOIL=1]
```

### 2. Leave nest

```
IF ant[SOIL=1]
    IF ant[POS=(0,$\boldsymbol{\theta}_0$)]
        $\mathrm{ant}_t$[POS=($\mathbf{r}_0$,$\boldsymbol{\theta}_0$)] → $\mathrm{ant}_{t+1}$[POS=($\mathbf{r}_0$+1, $\mathrm{HEAD}_0$)]
    END
END
```

### 3. Move

In this step probabilities for changing angle of heading and dropping soil are generated, and compared to a random number to determine whether they are acted upon or not.

```
IF ant[SOIL=1]
    If ant[$\mathrm{POS}_r$>0]

SlopeAhead = $\mathrm{cell}_{\mathbf{r},\boldsymbol{\theta}}$[HEIGHT] - $\mathrm{cell}_{\mathbf{r}+\gamma,\boldsymbol{\theta}+\mathrm{HEAD}}$[HEIGHT]
SlopeRight = $\mathrm{cell}_{\mathbf{r},\boldsymbol{\theta}}$[HEIGHT] - $\mathrm{cell}_{\mathbf{r}+\gamma,\boldsymbol{\theta}+\mathrm{HEAD}+\gamma}$[HEIGHT]
SlopeLeft = $\mathrm{cell}_{\mathbf{r},\boldsymbol{\theta}}$[HEIGHT] - $\mathrm{cell}_{\mathbf{r}+\gamma,\boldsymbol{\theta}+\mathrm{HEAD}-\gamma}$[HEIGHT]
```

`rand` is a random number 0-1.

```
If $\boldsymbol{\alpha}_{\mathrm{SlopeAhead}}$ > rand
    ant → ant[HEAD= HEAD+$\boldsymbol{\beta}$]
```

```
End

$\text{ant}[\text{POS}=(\mathbf{r},\boldsymbol{\theta})] \rightarrow \text{ant}[\text{POS}=(\mathbf{r}+1,\boldsymbol{\theta}+\text{HEAD})]$

If $\boldsymbol{\eta}_{\text{SlopeAhead},\mathbf{r}} > \text{rand}$
    Go to 4. Drop soil
Else
    end of turn for this ant
End
```

### 4. Drop soil

The soil dropped by an ant adds to the height of the cell which is the ant's current position ($\text{cell}_{\mathbf{r},\boldsymbol{\theta}}$):

$$\text{cell}_{\mathbf{r},\boldsymbol{\theta}}[\text{HEIGHT}] \rightarrow \text{cell}_{\mathbf{r},\boldsymbol{\theta}}[\text{HEIGHT} = \text{HEIGHT} + \boldsymbol{\omega}/\text{area}(\text{cell}_{\mathbf{r}})]$$

The ant remembers the angle at which the soil was dropped:

$$\text{ant}[\text{SOIL}=1,\ \text{HEAD},\ \text{MEMO}] \rightarrow \text{ant}[\text{SOIL}=0,\ \text{HEAD}=0,\ \text{MEMO}=\theta]$$

### 5. Search for nest

```
If ant[SOIL=0]
    If ant[$POS_r$>0]
        ant[POS=r,θ] → ant[POS=r−1,θ]
    End
End
```

### 6. Find nest

```
If ant[SOIL=0]
    If ant[$POS_r$=0]
        ant[POS=0,θ] → ant[POS=0,0]
    End
End
```

## Initial conditions

Ants:

```
[ID=n, SOIL=0, POS=0,0, HEAD=MEMO, MEMO=rand(1:100)]
```

Environments

| Environment | Experiments | Angle of incline | Radial cross section |
|---|---|---|---|
| 1 | x,t,y,z | 0° | flat |

| | | | |
|---|---|---|---|
| 2 | p,q | 15° | flat |
| 3 | a,b | 0° | sinusoidal |
| 4 | d | 15° | sinusoidal |

Supplementary table 1. For environment 1 (flat, level) the height of all cells is 0. For environment 2 which is at 15°, the height of the cells ranges from 26 to -26. For environment 3 which is level but has a sinusoidal cross-section, for the range $3<r<60$, $h=\sin(0.056*(r-4))$, otherwise $h=0$. Environment 4 is environment 3 rotated through 15°.

# Calculating change in direction of heading

$\boldsymbol{\alpha}$ gives the probability of turning a certain number of cells from 0-12 (either to the right or to the left) during one step forward. It is affected by the slope. As discussed in the results section of experiment 2, when on the level, the number of segments an ant turns out of its path to the left or right (for every one cell it goes forward) follows a Poisson distribution of mean 0.35 ($\chi^2=0.41$, df=2, p=0.81). As the model uses discretised angles-steps, this can easily be translated into probabilities of an agent turning though a certain number of cells for every one cell it goes forward; $\boldsymbol{\alpha}_{\text{level}}$ (supplementary table 2). 99% of turns observed were less than 45°, which translates to $\boldsymbol{\theta}=12.5$, so for the model the probability of turning more than 12 cells to the right or left in a timestep was set to zero. On a slope the observed distribution of turns did not follow a Poisson distribution ($\chi^2=214.0$, n=1355, df=2, p<0.001). The difference is due to fewer than expected ants making no turn, and more ants than expected making turns. For $\boldsymbol{\alpha}_{\text{slope}}$ the actual proportions making a turn of each magnitude is used, and the probabilities for the intermediate cells are interpolated.

The actual distance covered by these turns will increase with distance from the nest entrance because of the polar grid used, so these are approximations based on empirical results are pooled from all distances from the nest. We assume that the effects of the changing cell width with distance from the nest will cancel over the whole.

| Number of cells turned by ant, ***c*** during one timestep | Probability of exactly that number of cells being turned $\alpha_{\text{level}}$ | Probability of exactly that number of cells being turned $\alpha_{\text{slope}}$ |
|---|---:|---:|
| 0 | 0.27 | 0.21 |
| 1 | 0.22 | 0.18 |
| 2 | 0.17 | 0.15 |
| 3 | 0.12 | 0.13 |
| 4 | 0.074 | 0.10 |
| 5 | 0.052 | 0.078 |
| 6 | 0.038 | 0.057 |
| 7 | 0.024 | 0.036 |
| 8 | 0.010 | 0.015 |
| 9 | 0.0063 | 0.011 |
| 10 | 0.0046 | 0.011 |

| | | |
|---|---|---|
| 11 | 0.0026 | 0.010 |
| 12 | 0.00097 | 0.0098 |
| >12 | 0.00000 | 0.0000 |

Supplementary Table 2. The probabilities (**α**) of ant turning by a given number of cells (***c***) on a level surface or on a slope.

All ants on a `slope` $> \boldsymbol{g}$ will use the probabilities for a slope; others will use the probabilities for level ground.

As no left-right bias was observed (see results of Experiment 2), if slope $< \boldsymbol{g}$, the direction of turn will be chosen at random. If `slope` $< \boldsymbol{g}$ ants are more likely to turn downhill.

| Probability | Level | | Slope | |
|---|---|---|---|---|
| | Right | Left | Uphill | Downhill |
| ***b*** | 0.5 | 0.5 | 0.58 | 0.42 |

Supplementary Table 3. Probability of turning in the specified direction (***b***).

Let **β** represent the change in heading. To determine **β**, first the slopes ahead (straight on, to the left one cell and to the right one cell) are detected. Then the probabilities (**α**) are used to determine the magnitude (***c***) of the turn. Then, if the magnitude is greater than zero, the direction (**b**) is determined, so **β** has a magnitude in cells and a direction (positive turns to the right, negative to the left). `abs` is the absolute gradient of the slope, without sign.

```
SlopeAhead = $cell_{r,\theta}$[HEIGHT] - $cell_{r+1,\theta+HEAD}$[HEIGHT]
SlopeRight = $cell_{r,\theta}$[HEIGHT] - $cell_{r+1,\theta+HEAD+1}$[HEIGHT]
SlopeLeft = $cell_{r,\theta}$[HEIGHT] - $cell_{r+1,\theta+HEAD-1}$[HEIGHT]

If abs(SlopeAhead) > $\mathbf{g}$
    $\boldsymbol{\alpha}_{c} = \boldsymbol{\alpha}_{c,slope}$
Else
    $\boldsymbol{\alpha}_{c} = \boldsymbol{\alpha}_{c,level}$
End
```

A random number 0-1 is compared to $\boldsymbol{\alpha}_c$ to find **c**, the magnitude for $\boldsymbol{\beta}$. A second random number 0-1, `rand`, is used as below to determine the direction of $\boldsymbol{\beta}$, where positive numbers are turns to the right, and negative to the left. If **c** = 0, the direction has no effect. In the code given here right is tested first for simplicity– in the full code the order of testing right versus left is randomised.

```
If abs(SlopeAhead) > $\mathbf{g}$
        If SlopeRight < $-\mathbf{g}$
        If rand < $\mathbf{b}_{\mathrm{Downhill}}$
        $\boldsymbol{\beta} = \mathbf{c}$
        Else
        $\boldsymbol{\beta} = \mathbf{c}*-1$
        End
    Else if SlopeLeft < $-\mathbf{g}$
        If rand < $\mathbf{b}_{\mathrm{Downhill}}$
        $\boldsymbol{\beta} = \mathbf{c}*-1$
        Else
        $\boldsymbol{\beta} = \mathbf{c}$
        End
    End
Else if rand < $\mathbf{b}_{\mathrm{Right}}$
$\boldsymbol{\beta} = \mathbf{c}$
Else
$\boldsymbol{\beta} = \mathbf{c}*-1$
End
```

## Calculating probability of dropping soil

The probabilities of dropping soil at a given distance from the nest are determined by the logistic function:

```
$\eta_r$=(d*(abs(r/r0)^(abs(f))))/(1+((abs(r/r0))^(abs(f))))
```

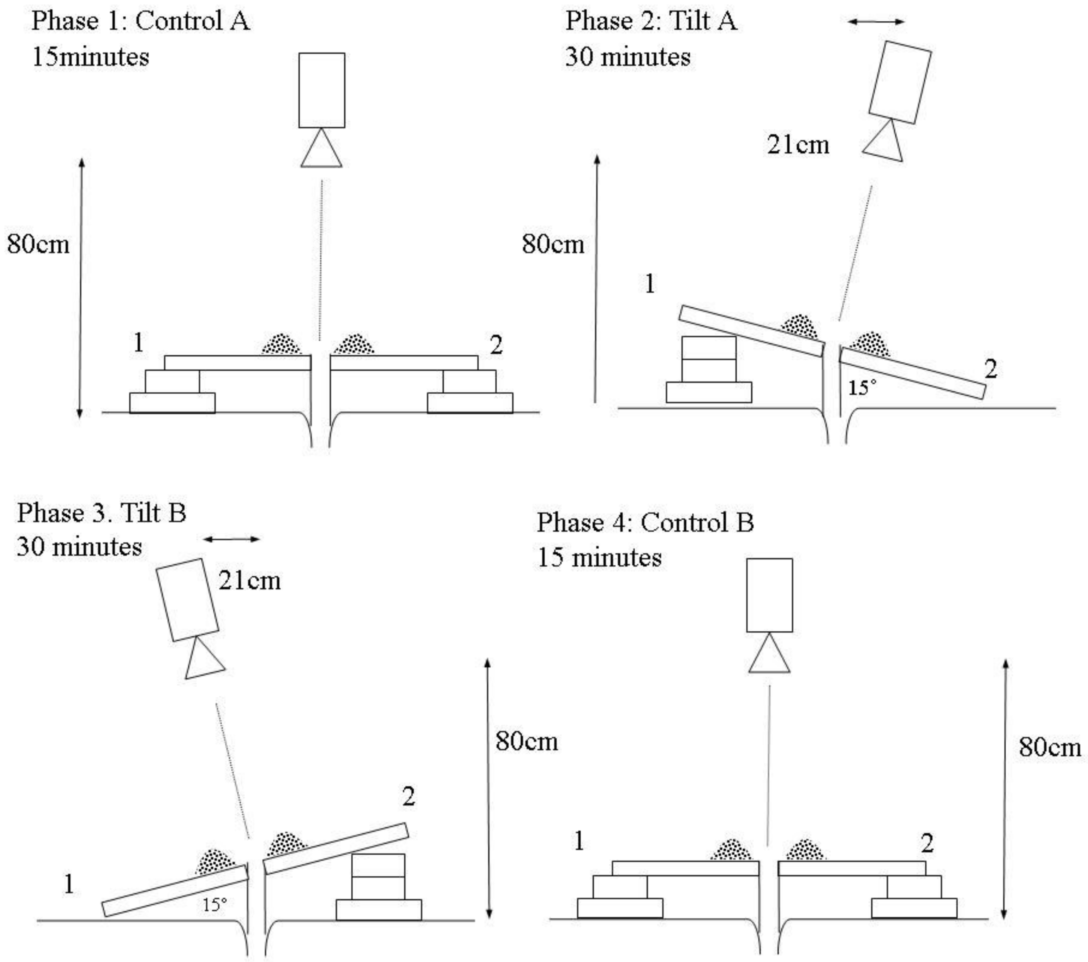
The parameters have been estimated from empirical data for both level and sloping environments:

$\mathbf{d}_{level}$ **=** 1.05 ($p<0.0001$), $\mathbf{f}_{level}$ **=** -3.28 ($p<0.0001$), $\mathbf{r0}_{level}$ **=** 19.98 ($p<0.0001$)

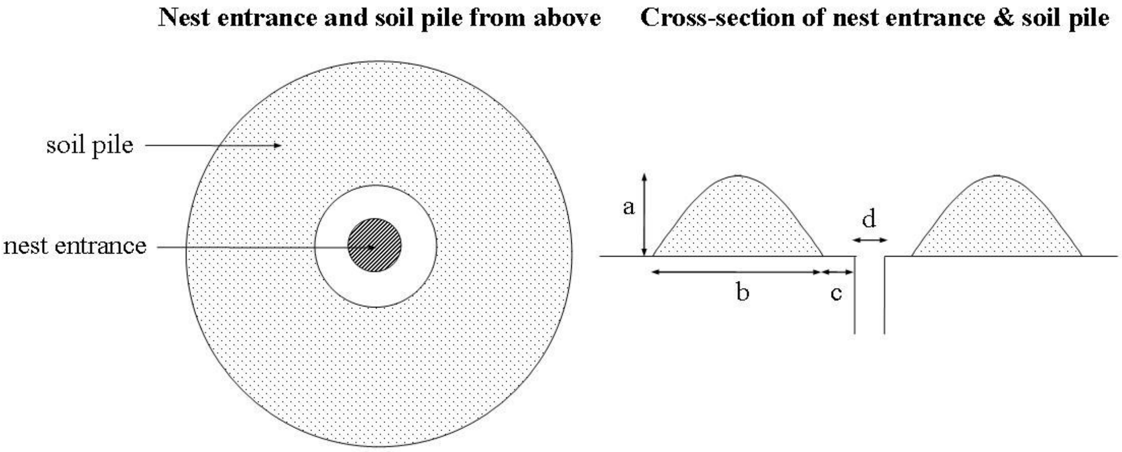
$\mathbf{d}_{slope}$ **=** 1.12 ($p<0.0001$), $\mathbf{f}_{slope}$ **=** -2.92 ($p<0.0001$), $\mathbf{r0}_{slope}$ **=** 25.11 ($p<0.0001$)

```
If abs(SlopeAhead) > g
        $d = d_{slope}$
        $f = f_{slope}$
        $r0 = r0_{slope}$
Else
        $d = d_{level}$
        $f = f_{level}$
        $r0 = r0_{level}$
End
```

## Supplementary Figures



Supplementary Figure 1. Phases of Experiment 1. Platform connected to nest entrance with a vertical tube. For Phases 2 and 3 the platform was tilted and the camera moved. 1 and 2 at the end of the platform indicate the directions of soil dumping used in analysis.


Nest entrance and soil pile from above

Cross-section of nest entrance & soil pile

Supplementary Figure 2.

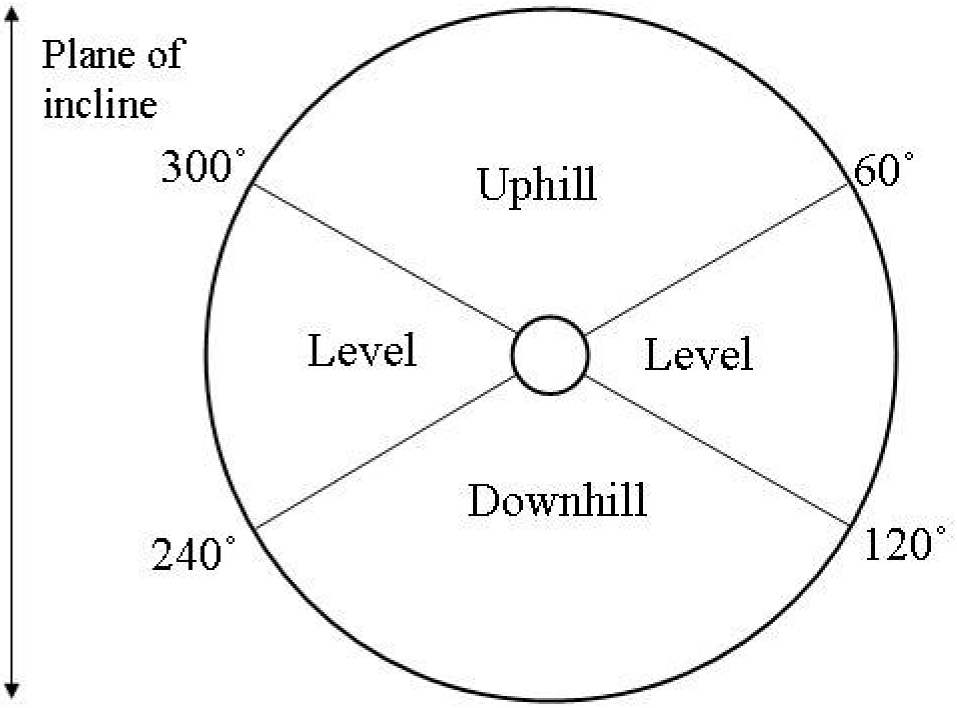
Shape and dimensions of *P. ambigua* soil piles (range, mean± SD, *N*=10).

a= height of mound: 4-10mm, 7.5± 2.1mm.

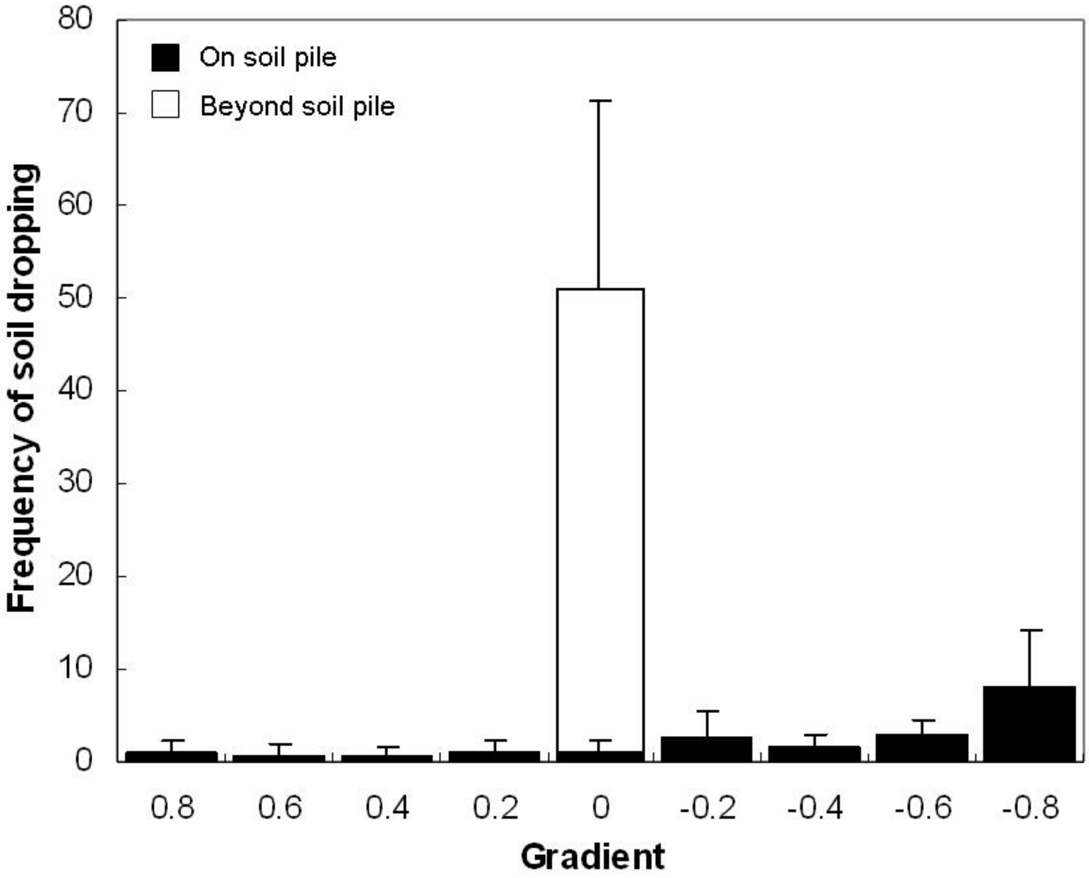
b= width of mound: 8-30mm,16.5± 7.9mm.

c= gap between mound and nest entrance: 1-3mm, 1.9± 0.7mm.

d= diameter of nest entrance: 3-7mm, 5.1± 1.3mm.



Supplementary Figure 3. Division of platform into equal sectors of 120° in total (uphill, downhill and level) for analysis.



Supplementary Figure 4. The number (mean +SD) of ants dropping soil at each local gradient, both on the artificial soil pile and beyond it. No ants dropped their soil before reaching the artificial pile.