



# Subterranean nesting behaviour in response to soil moisture conditions in the southern ant, *Monomorium antarcticum* Smith (Hymenoptera: Formicidae)

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## ABSTRACT

The New Zealand endemic southern ant (*Monomorium antarcticum*) excavates subterranean nests in various soil types, with brood distributed throughout excavated cavities connected by tunnels. Because cavities are often constructed near the soil surface, variation in rainfall patterns will affect soil moisture, and potentially lead to regular flooding of cavities. We examined how *M. antarcticum* make colony emigration decisions as soil moisture changes over time, and investigated how colonies manage brood underground during simulated rainfall events. We show that colonies will emigrate to wetter soil and excavate a new nest when their environment becomes too dry. After we add water to the surface of the nest (i.e. simulate rainfall), workers transport brood from cavities into tunnels, and move them back into the cavities as soon as the 'rain' stops. Workers tend to prioritise moving brood from cavities with higher densities of brood, regardless of the depth of the cavity from the soil surface. We discuss how the ability to emigrate in response to changes in soil environment, and to effectively respond to unpredictable rainfall/flooding events, can help us understand how this species persists in a wide-range of habitat types.

## KEYWORDS

Brood management; colony emigration; nest construction; flooding; soil moisture

## Introduction

Subterranean ant species are capable of excavating elaborate nests that are comprised of a series of tunnels and cavities for storing brood or colony resources (Tschinkel 1999, 2015). However, this excavation effort should not be mistaken for construction of a permanent home, as nest emigration is common among excavating ant species (McGlynn 2012). That is, when a colony is ready to reproduce, or when conditions become sub-optimal, a colony may abandon its nest and relocate (re-excavate) a new nest.

Subterranean nesting behaviour can optimise the rearing of offspring. Cavities and tunnels offer shelter from predators and weather, and workers can shift brood during ephemeral changes in temperature or rainfall, providing a consistent microclimate for developing brood (Tschinkel 2015). For example, *Camponotus mus* and *Solenopsis invicta* colonies transport eggs and larvae up and down a temperature gradient within their nest mound in a predictable diurnal pattern that corresponds to daily temperature fluctuation (Roces & Núñez 1989; Penick & Tschinkel 2008).

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Subterranean ant species have evolved coping mechanisms to ensure that adults and brood avoid flooding during rainfall events. For example, *Pheidole cephalica* workers engage in alarm running throughout the colony, alerting other nest mates of the presence of water outside the nest entrance (Wilson 1986). *Polyrhachis sokolova*, a mud-nesting ant, experiences daily flooding that coincides with high tides in mangroves (Nielsen 1997). In this system, narrow tunnels that connect the main cavities of the nest can maintain air pockets – even during high tide – suggesting that flooding in one part of the nest does not mean the entire nest is flooded.

*Monomorium antarcticum* (the endemic New Zealand ‘southern ant’) constructs a series of subterranean tunnels and cavities for rearing brood (Figure 1). The southern ant is one of NZ’s most widely distributed and abundant ant, present in areas of very high (e.g. Fiordland: 8000 mm) and very low (e.g. Canterbury: < 500 mm) rainfall per year, and on nearly all of NZ’s islands (Don 2007). Colonies can be found under half-buried stones or logs in open pastures, grasslands, swamps at high altitudes, forests, and gardens. Despite how common they are, very little is known of their nesting ecology. Here, we monitor subterranean nesting behaviour in southern ant colonies by observing their (1) emigration patterns as soil moisture changes over time, and (2) brood management underground during simulated rainfall events, to enhance our understanding of how these ants can utilise so many different habitats.

## Methods

### Colony collection and maintenance

Four colonies (hereafter colonies A, B, C, and D) of *M. antarcticum* were collected from pasture land in St. Arnaud, South Island, NZ in March 2016. We located colonies by turning over rocks that were  $\geq 50\%$  buried in soil. Colonies used in this study had all built their nests under soil but adjacent to the side of the rock, approximately 1–3 cm below the soil surface (Figure 1). To remove colonies, ~3–5 cm of soil around (and including) the nest cavities was excavated to maximise collection of brood (which tend to be clustered in cavities) and workers (which can be distributed throughout cavities and tunnels). Soil, ants and brood were placed in a single container and brought back to the Animal Rearing Facility at the Zoology Department at Otago University. To separate colonies from the soil,



**Figure 1.** Subterranean nest cavities *in situ* by *Monomorium antarcticum*. Cavities were exposed by removing a half-buried rock. Photo taken by SDL, 15 November 2017, Swampy Summit, Dunedin, NZ. The tape measure (for scale) is in cm.

queen(s), workers, and brood were aspirated into collecting vials (diameter 3.2 x height 7.6 cm). For all experiments and trials, when colonies (queens, workers and brood) were aspirated and separated from soil, they remained in vials for less than 20 min (approximately the length of time needed to collect the entire colony).

Ant colonies were housed in separate plastic bins (width 28 x length 44.5 x depth 13 cm), at a constant temperature of 25° C, and a 12:12 h light: dark cycle with a simulated gradual 1h dawn and dusk cycle each morning and evening respectively. Bins were lined around the top edges with Pro-lon PTFE 901 polymer<sup>®</sup> paste to prevent escape. Inside their bin, colonies were provided with 50% sugar water *ad-libitum* and two lab-reared mealworms (*Tenebrio molitor*) for protein every two days. Sugar water and mealworms were placed haphazardly in the bin, outside of the farms. Colonies were checked daily.

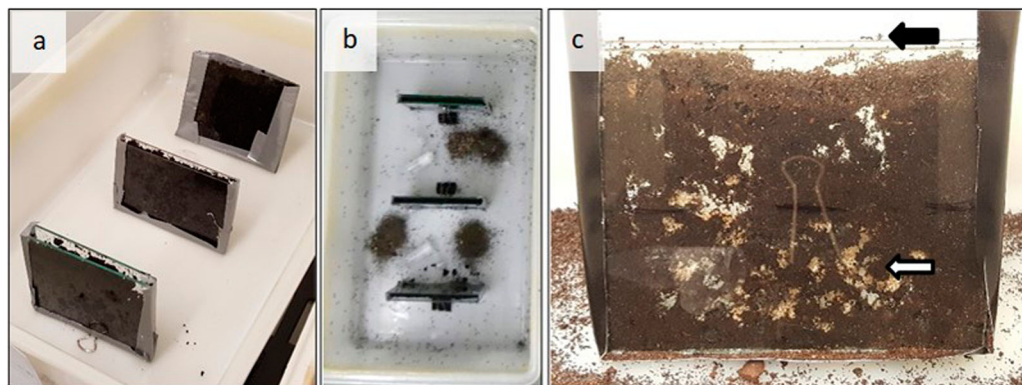
### Experiment 1: emigration patterns as soil moisture changes over time

We constructed three ant farms (length 11 cm x height 9 cm x width 0.7 cm) for each of three colonies (A, B, and C) on 28 April 2016 (trial 1) and 28 May 2016 (trial 2). The three ant farms stood vertically inside each colony's bin (Figure 2(a)). The farms were filled with ~40 g soil collected from a yard in a residential neighbourhood of Dunedin, NZ. Industrial tape held the glass panes of the farm together. For each trial, we randomly assigned each farm in the bin to one of three watering treatments: 0 mL: farm soil received no additional water throughout the experiment; 5 and 10 mL: farm soil received 5 mL (~1 mL per 8 g soil) or 10 mL (~1 mL per 4 g soil) of water along the upper surface area of the farm every two days of the experiment. We added water evenly across the surface using a 3mL pipette.

Once the farms were set up, we introduced colonies to the bins by pouring out queen(s), workers, and brood that had been contained in the collecting vials into the bin (outside the farms; Figure 2 (b)). Watering treatments began one day after we introduced colonies to the bins, and data collection began the following day.

To determine whether ant colonies emigrated, we recorded whether brood were visible (1) or absent (0) from subterranean chambers when viewed from either side of the farm. Presence of brood in the subterranean chambers that the ants had excavated in each of the ant farms (Figure 2(c)) indicates that the environment is suitable for nesting. In trial 1, brood data were collected on days 2, 5, and 22; in trial 2, brood data were collected every day for 22 days.

In trial 2, we also recorded foraging effort to determine if that could be used to predict whether colonies would emigrate to different farms. Foraging effort was calculated as the number of



**Figure 2.** Experiment 1 Set-up (Colony B shown here). (a) For each colony, three farms were set-up in a plastic bin lined with polymer paste to prevent escapees (see methods). (b) Birds eye view of set up showing adults and brood when introduced to the bin. (c) Farms were checked for presence of brood (white arrow) under the soil surface and adult activity (black arrow) above the soil surface.

individuals present on the upper surface area of each farm (Figure 2(c)) on the days in between watering treatments. Foragers were counted twice, counts were averaged, and the value was rounded to the nearest whole number.

In between trials 1 and 2, we destroyed and set-up new farms, and re-randomised the location of watering treatments. To destroy farms, we opened the two plates of glass and aspirated adults and brood to separate them from the soil. We cleaned the bins and wiped them with ethanol. New soil was collected from the same yard in Dunedin, however, the second soil collection occurred after a heavy rainfall event, so soil was naturally wetter at the beginning of trial 2. Due to the low rate of sampling in trial 1 and difference in initial soil moisture between both trials, we treat trial 1 data as pilot data.

## **Experiment 2: brood management underground during simulated rainfall events**

On 21 June 2016, we destroyed all farms (see Experiment 1) and placed one large ant farm (length 30 cm x height 16 cm x width 0.7 cm) in the centre of each colony's bin (Figure 3(a)). We filled farms with ~180 g of soil (from the same yard as Experiment 1) and introduced the colony. Based on the results from Experiment 1, we estimated that preferred soil moisture in the ant farms to be ~1 mL per 6 g of soil every other day. For 180 g soil in the large farms, this would be maintained by adding ~30 mL of water to the farms every other day. We applied water evenly across the top surface of the farm using a 3 mL pipette. Adding water to the nest took approximately 1–2 min. The queen in colony C died before data were collected for Experiment 2, so Experiment 2 was conducted on colonies A, B, and D.

On 13, 15, and 17 September (trial 1), we monitored how ants moved brood in their subterranean cavities during and after simulated rainfall (during the water application to the surface of the farm). On 25 September 2016, we destroyed and set-up farms with fresh soil, and monitored cavity excavation for two weeks. On 7, 9, and 11 October (trial 2), we repeated the observations of brood movement in subterranean cavities during and after simulated rainfall.

For each brood movement trial, we photographed (Panasonic Lumix DMC-FZ300 camera with a 24X (25–600 mm) full-range F2.8 aperture Leica Lens) colonies at four different time points: Before watering immediately before watering, 0 min: immediately after watering, 10 and 20 min: time after watering. We took each photograph approximately 1 m away on the same side of the ant farm each time.

We processed all photographs using the image processing analysis software ImageJ ver. 1.50i (Schneider et al. 2012). For each trial, we used the first image of a colony as a reference image and labelled each distinct brood cavity. For all images, we calibrated each photo to 5 cm on a ruler in the photo using the inbuilt 'scale function.' We measured the total area of each identified brood cavity and the total area of brood within each cavity for all four time points in each trial. We also measured the depth from the surface of each brood cavity for each trial before we added water (Before watering). Due to high variation in presence/absence of brood within brood cavities, we only include those cavities that contained 0.1 cm<sup>2</sup> of brood in at least 75% of recorded time points. We calculated the change in brood area within each cavity during the rainfall (suggesting brood transport into or out of the cavity) by taking the difference in brood area between adjacent time points; i.e. Before–0 min, 0–10 min and 10–20 min.

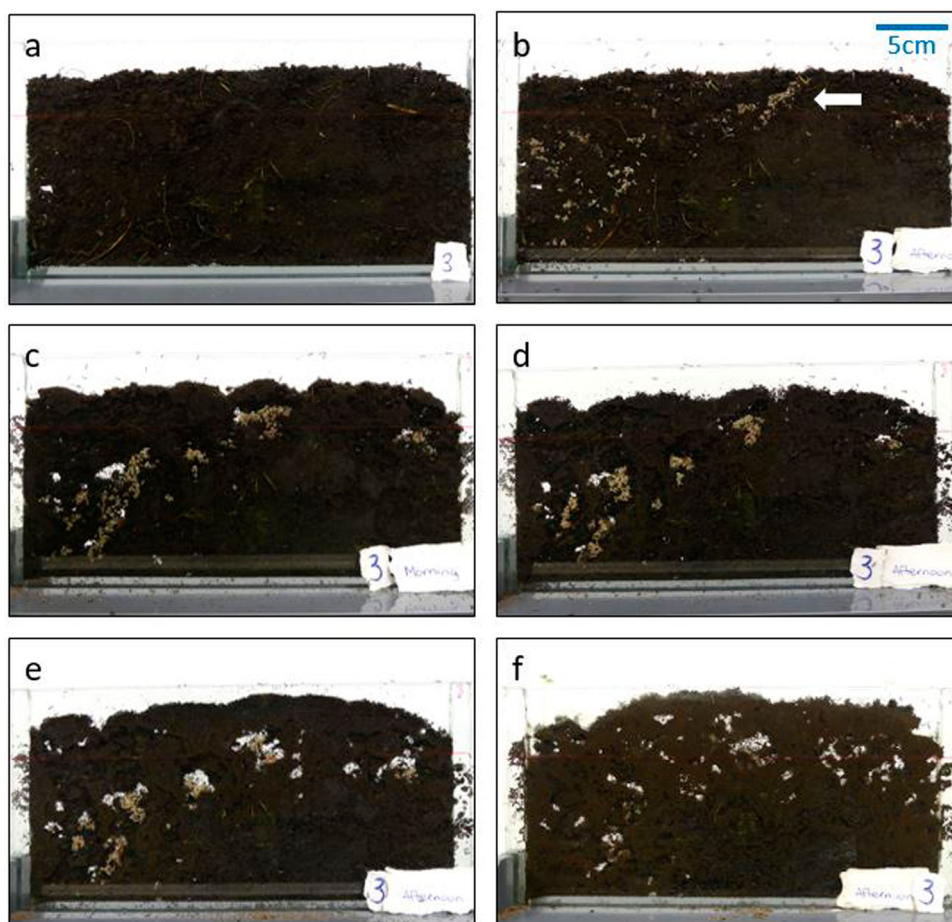
## **Statistical analyses (Experiments 1 and 2)**

We conducted all statistical analyses in R (ver. 3.4; R Core Team 2017).

### **Experiment 1**

We ran generalised linear mixed models (GLMM) on Experiment 1 data (using the *glmer* function in the *lme4* package; Bates et al. 2011), where treatment category (0, 5 and 10 mL), day, and the





**Figure 3.** Experiment 2: Example of progression of ant colony cavity excavation over two weeks (Colony B shown here). (a) Day 1, before ants are introduced to the bin. (b) 3 h after ants are introduced to the bin (note presence of brood, white arrow). (c) 18 h after introduction. Cavities start to become apparent, workers begin condensing brood into clumps, (d) 26 h after introduction. Brood are sorted into specific condensed clumps. (e) 50 h after introduction. Workers excavate and enlarge cavities surrounding brood clumps. (f) 2 weeks after introduction. Many cavities observed in (e) with brood still contain brood two weeks after the ants began excavating. The bar in (b) represents a 5 cm scale that applies to all images.

interaction between treatment and day were included as fixed factors, and colony was included as a random factor. To compare how colonies decided where to move brood over time, we ran a GLMM with a binomial distribution (logit-link), where the binary response variable was either the presence (1) or absence (0) of brood inside excavated cavities in an ant farm. To compare if forager effort on each farm changed over time, we ran a GLMM with Poisson distribution (log-link), and the response variable as the number of individuals present on each of the farms on each day.

### Experiment 2

We ran a generalised linear model (GLM) on each trial separately in Experiment 2. To determine how change in brood area varied across adjacent time points, we ran GLM with normal distribution (identity-link), where the difference in brood area between adjacent time points was used as the response variable, and adjacent time points (i.e. Before–0 min, 0–10 min and 10–20 min), cavity depth (cm) from the surface, initial brood area (cm<sup>2</sup>) in the cavity, colony (A, B, D), and day of observation were included as fixed factors. We found evidence to suggest cavity size was correlated

with cavity depth (trial 1;  $P = 0.034$ ) and brood area (trial 2;  $P < 0.001$ ); therefore, we did not include cavity size in the models.

Results

Experiment 1: emigration patterns as soil moisture changes over time

In trial 1, we noticed that colonies gradually moved their brood between farms: from 0 mL farms to 5 or 10 mL farms (Figure 4). In trial 2, colonies transferred their brood from ‘low’ (0–5 mL) to ‘moderate/high’ (5–10 mL) watering treatment over time (GLMM: trt:  $F_{2,191} = 13.57$ ,  $P < 0.001$ ; day:  $F_{1,191} = 1.18$ ,  $P = 0.28$ ; trt x day:  $F_{2,191} = 5.89$ ,  $P = 0.003$ ; Figure 4). By the end of trial 2, none of the colonies had brood in the 0 mL farm; colonies A and C moved all of their brood into the 5 mL farm, whereas colony B split brood between the 5 and 10 mL farm. We calculated soil moisture preference for brood rearing as 1 mL water: 6 g soil (observed preference: 5–10 mL per 40 g of soil; ratio: 1 mL water: 4–8 g soil; average: 1 mL water: 6 g soil).

In trial 2, the proportion of ants inspecting the surface of 0 mL farms decreased over time, whereas the proportion inspecting the 5 or 10 mL farms increased (GLMM; trt:  $F_{2,92} = 1.42$ ,  $P = 0.25$ ; day:  $F_{1,92} = 31.71$ ,  $P < 0.001$ ; trt x day:  $F_{2,92} = 7.10$ ,  $P = 0.001$ ; Figure 5).

Experiment 2: brood management underground during simulated rainfall events

After simulated rainfall (time 0), we observed workers quickly grabbing larvae and ‘tossing’ them down vertical shafts or placing them into horizontal tunnels. In both trials, at time 0, workers transported brood out of cavities, regardless of cavity depth, and moved most of the brood back into cavities by time 10 (GLM factor- time points: trial 1:  $F_{2,136} = 9.70$ ,  $P = 0.0001$ ; trial 2:  $F_{2,127} = 13.54$ ,  $P <$

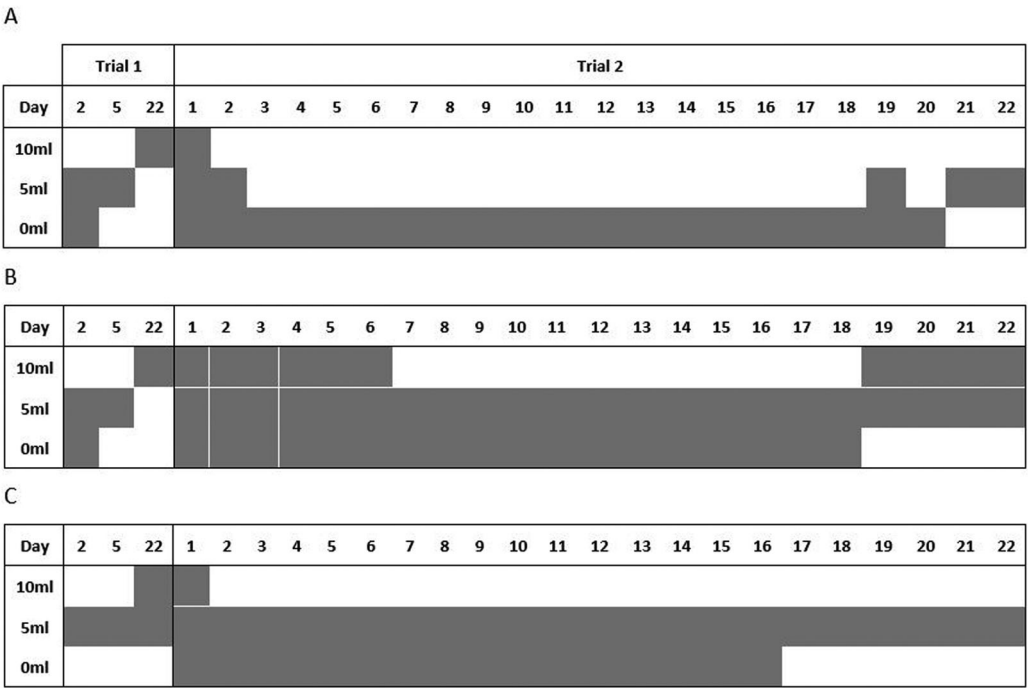
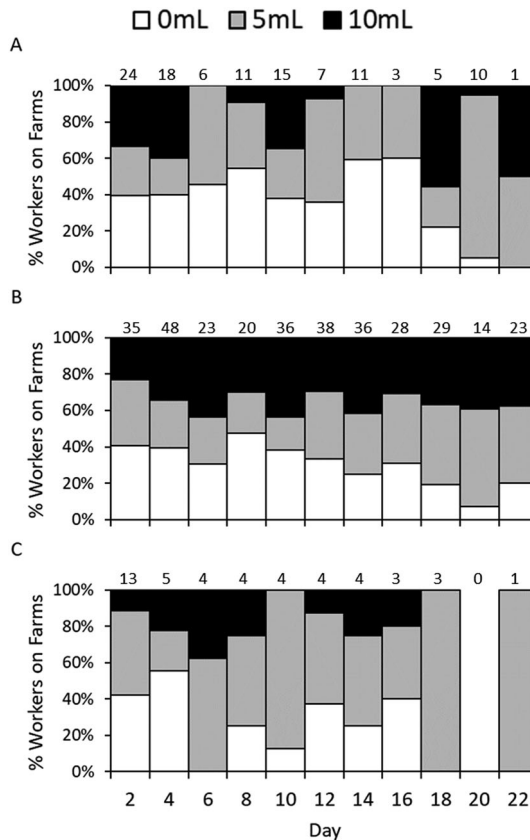


Figure 4. Experiment 1 – distribution of the presence of brood across farms for (a) colony A, (b) colony B, and (c) colony C on days 2, 5, and 22 in trial 1, and each day 1 through 22 in trial 2. Grey squares represent the presence of brood.



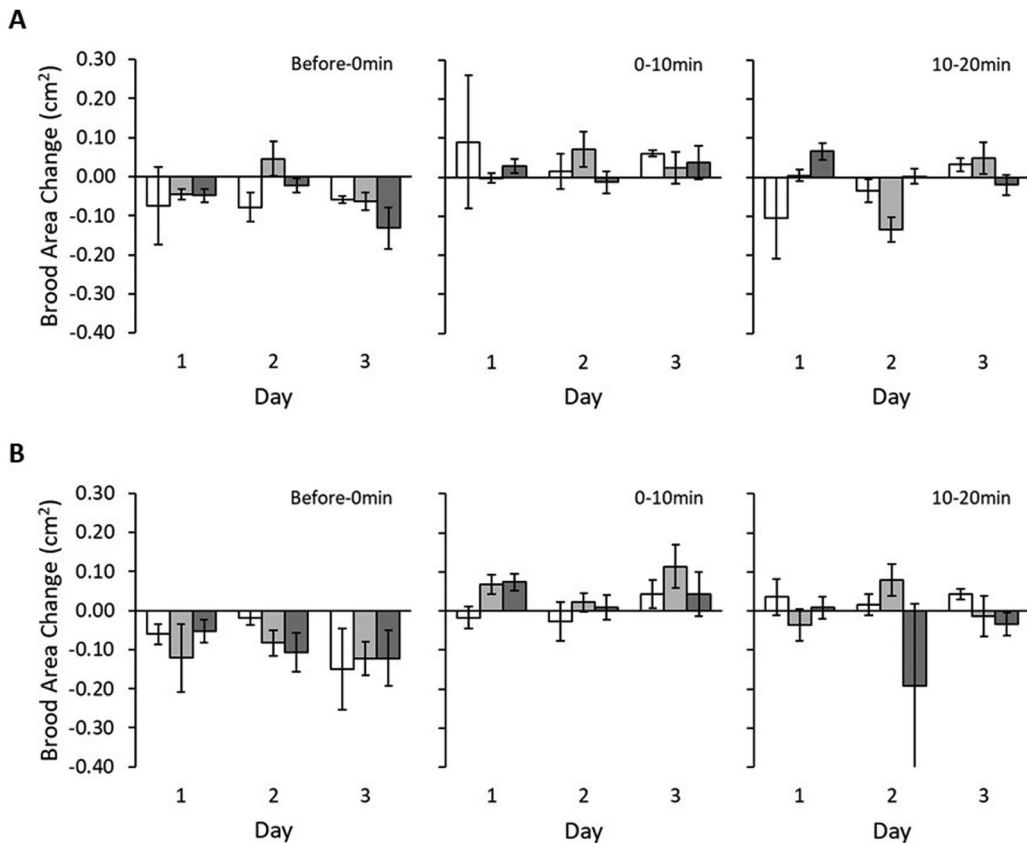
**Figure 5.** Experiment 1, trial 2 – percentage of workers that were out of the nest from (a) colony A, (b) colony B, and (c) colony C, walking along the top of the farm that received 0 mL (white), 5 mL (grey) or 10 mL (black) water. Workers were counted twice, and the average used for analyses. The average total number of workers observed across all three farms is shown above each bar. Data were recorded on days in between simulated rainfall events.

0.0001; Figure 6). The initial area of brood in the cavity at the start of the time point also predicted brood movement, i.e. cavities with more brood had more brood removed immediately after rainfall, and cavities with less brood had more brood added to them 20 min after rainfall (GLM factor- initial brood area: trial 1:  $F_{2,136} = 16.38$ ,  $P < 0.0001$ ; trial 2:  $F_{1,127} = 18.52$ ,  $P < 0.0001$ ). None of the other factors were significant predictors of brood movement in either trial (trial 1: colony  $F_{2,136} = 0.13$ ,  $P = 0.88$ , day  $F_{2,136} = 0.52$ ,  $P = 0.47$ , cavity depth  $F_{2,136} = 0.06$ ,  $P = 0.81$ ; trial 2: colony  $F_{2,127} = 0.76$ ,  $P = 0.47$ , day  $F_{2,127} = 0.07$ ,  $P = 0.80$ , cavity depth  $F_{2,127} = 0.67$ ,  $P = 0.42$ ).

Between trial 1 and trial 2, we destroyed the farm and observed cavity excavation. Within three hours after introducing the colony to the large ant farm, workers had transported brood into the ant farm (Figure 3(b)). Within 50 h, cavity shape and size were established, and brood were concentrated into specific cavities (Figure 3(b–e)). After two weeks, the cavities observed after 50 h were still recognisable and still contained brood (Figure 3(f)).

## Discussion

Here we describe the nesting ecology of *Monomorium antarcticum*, and observe colony emigration as soil moisture changes and subterranean brood movement during simulated rainfall. In our first experiment, we confirm that, like many other species of subterranean ant (McGlynn 2012), *M. antarcticum* will excavate a new nest-site and relocate their brood should conditions of their



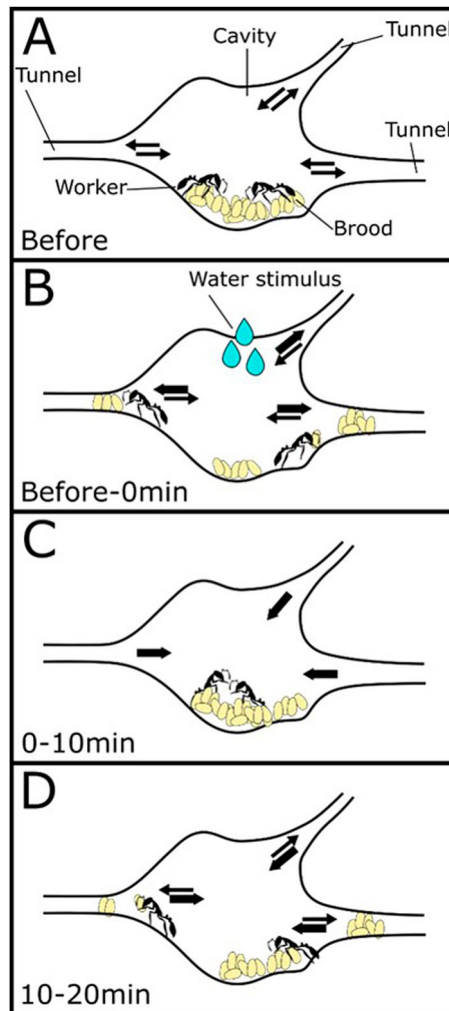
**Figure 6.** Experiment 2 – average change in brood area ( $\pm$  se) across brood cavities (cm<sup>2</sup>) in each colony, day of the trial, and time point: Before-0 min, 0–10 min, and 10–20 min. (a) Data from trial 1. (b) Data from trial 2. White bars represent colony A, grey bars represent colony B, dark grey bars represent colony D.

previous location become sub-optimal (i.e. too dry). The ability to relocate quickly is likely due to the consistent exploratory behaviour of workers. Our results show that as soil conditions for nesting become sub-optimal, the proportion of the worker activity on those soil types declines as well.

We also explored the subterranean behaviour of the colony during a simulated rainfall event – common in many of the locations where these ants are naturally found. Like other ant species that experience flooding (Wilson 1986; Nielsen 1997), *M. antarcticum* responded by immediately increasing worker activity and shifting brood into the tunnels. Unlike *Camponotus mus* and *Solenopsis invicta* that transport subterranean brood vertically in response to daily temperature fluctuation (Roces & Núñez 1989; Penick & Tschinkel 2008), there was no evidence that *M. antarcticum* workers focused on brood from cavities closer to the soil surface first after a rainfall event. Instead, workers focused on brood from bigger piles, and moved them into the horizontal tunnels or dropped them into vertical shafts first. After the rainfall event ceased, workers began moving brood back into cavities – emptier cavities receiving more brood – after which, there was additional spatial sorting of brood among the cavities over the next 20 min (Figure 7). These behaviours are likely the result of stigmergy: self-organised interactions between the ants and brood affected by the size or type of stimulus instead of a fixed action pattern in response to a rainfall event (Theraulaz et al. 1998).

*Monomorium antarcticum* colonies can be found throughout New Zealand in open pastures, grasslands, swamps, forests, sand, and gardens (Don 2007). While it has been hypothesised that what is called *M. antarcticum* may actually be three or four distinct ‘species’ (Jones et al. 1988;





**Figure 7.** Graphical representation of brood movement during a rainfall event, based on data from Experiment 2. The thickness of arrows indicates the predominant direction. (a) 'Before' the simulated rainfall event, workers transport brood between chambers at ambient levels. (b) Immediately following the simulated rainfall event, ('Before-0 min'), workers rapidly move brood out of the cavities into adjoining tunnels. (c) By 10 min after the rainfall event ('0-10 min'), workers transport brood back into cavities. (d) At 20 min after the rainfall event ('10-20 min'), brood is still brought into the cavities, though workers also begin shifting brood among cavities again (a).

Wang & Lester 2004), it is clear that colonies are capable of nesting in a variety of soil types (including soil, clay, and even sand) in regions with variable rainfall or 'flooding' events. We provided food for the ants in this study outside of the ant farm, and show that above-ground foraging activity was linked to brood relocation (and nest emigration). In the field, finding workers above ground is rare, and flipping every half-buried rock (upon locating a population of ants) became the most efficient method of locating colonies. It is likely that many foragers scavenge for seeds and other nutrients inside the soil itself. In other words, even though *M. antarcticum* can forage above ground, many likely rely on foraging below ground. This means that the substrate in which they construct their nests may affect a variety of life history characteristics, not just those regarding placement of brood.

Ants can construct their cavities among dense root systems (e.g. of grasses), which can maintain structural support of nest cavities during disturbances, such as flooding events (Nielsen 1997; Cassill et al. 2002; Laskis & Tschinkel 2009). In our study, we separated the ant adults and brood from the

soil and roots where cavities were naturally constructed before introducing them to an unfamiliar soil type in the ant farms. We found that cavity and tunnel structure/integrity were quite robust to simulated rainfall events. This ability to reinforce the soil cavity structure is also observed in *Temnothorax rugatulus* ants, who will adjust the nest architecture in response to changes in humidity and air flow, and build thicker walls around areas with more brood (DiRienzo & Dornhaus 2017).

Because *M. antarcticum* are distributed across a variety of environments throughout the North and South Island of New Zealand, it is unknown how different populations have adapted to different soil types. If these populations are indeed the same species, can they adjust their behaviour, including foraging, subterranean nest construction, and brood movement during disturbance, in different soil types? On the other hand, if *M. antarcticum* is instead a 'complex', comprised of multiple species (Wang & Lester 2004), then perhaps different species are limited to specific habitats or soil types. Here we confirm that *M. antarcticum* collected from a population in the Nelson region will emigrate in response to changes in soil moisture and quickly move brood into tunnels during rainfall/flooding events, strategies that have likely allowed this species to persist in a wide-range of habitat types throughout New Zealand.

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## Disclosure statement

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