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Cite this article: Bardunias PM, Calovi DS, Carey N, Soar R, Turner JS, Nagpal R, Werfel J. 2020 The extension of internal humidity levels beyond the soil surface facilitates mound expansion in *Macrotermes*. *Proc. R. Soc. B* **287**: 20200894.
http://dx.doi.org/10.1098/rspb.2020.0894

Received: 20 April 2020
Accepted: 16 June 2020

Subject Category:
Behaviour

Subject Areas:
behaviour, biomaterials, cognition

Keywords:
airflow, template, humidity, construction, *Macrotermes*, termite

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The extension of internal humidity levels beyond the soil surface facilitates mound expansion in *Macrotermes*

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Termites in the genus *Macrotermes* construct large-scale soil mounds above their nests. The classic explanation for how termites coordinate their labour to build the mound, based on a putative cement pheromone, has recently been called into question. Here, we present evidence for an alternate interpretation based on sensing humidity. The high humidity characteristic of the mound's internal environment extends a short distance into the low-humidity external world, in a 'bubble' that can be disrupted by external factors like wind. Termites transport more soil mass into on-mound reservoirs when shielded from water loss through evaporation, and into experimental arenas when relative humidity is held at a high value. These results suggest that the interface between internal and external conditions may serve as a template for mound expansion, with workers moving freely within a zone of high humidity and depositing soil at its edge. Such deposition of additional moist soil will increase local humidity, in a feedback loop allowing the 'interior' zone to progress further outward and lead to mound expansion.

1. Introduction

Termites in the subfamily Macrotermitinae construct large, elaborate mounds of soil above their colonies [1]. The morphology of these structures is thought to play a key role in driving the evolution of eusociality in many species [2]. These mounds are so integral to their physiology that they can be viewed as an extension of the physical form of the insects [3]. The architecture of the mound makes use of temperature differentials to drive ventilation [4]. This is thought to play a role in maintaining symbiotic fungus gardens that will only grow over a narrow range of environmental conditions [5–8]. For all of the obvious wonder of these structures, very little is known about how individually minute and blind insects come together to construct their mounds.

The formation of mounds in *Macrotermes* spp. is a product of two phases of building, which may or may not rely on the same underlying mechanisms [9]. Mound expansion occurs as soil is moved from within or beneath the mound and deposited on the outer surface, while conduits within the mound may be excavated or remodelled without removing soil from the mound. Progressive building with soil of the type seen in mound expansion has been described

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5036531.

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through a mechanism called stigmergy, an indirect mode of communication whereby the work product of a builder acts to guide subsequent workers. Grassé [10] suggested that termite workers mark parcels of soil with a scent—a putative 'cement pheromone'—as they place them, with each addition of marked soil enhancing the signal from the aggregate. In this interpretation, the scent label performs two functions [11]. First, the diffusion gradient of the scent acts as an attractant, providing information that orients termites towards the work site. Second, a threshold level of this cement pheromone triggers pellet-dropping behaviour in the termites and leads to an aggregation of pellets. Models based on a cement pheromone system have been shown to produce pillars or gallery structures [12–14]. However, these models typically do not consider excavation or how the pheromone might affect the choice of digging site, and experiments have shown that the scent of freshly deposited soil also elicits digging [11,15]. If termites were equally influenced by cement pheromone to deposit or remove pellets from the same locations, one would expect that coherent structures would not form. Other studies suggest a role for tactile interaction with the environment and the topography of build sites, either to supplement scent labelling [16,17] or in place of scent labelling [18,19], indicating that a model based on scent only is incomplete.

Bruinsma [11] revealed a key challenge to the cement pheromone-mediated model of building by *Macrotermes* when he showed that week-old soil produces as strong a reaction as freshly manipulated and labelled soil. A rapid decay rate for cement pheromone is required to focus termite labour at the site of new deposition. Termites on mounds must walk over the previous build to get to the site of the new expansion. If old soil around a build site is as likely to trigger dropping behaviour as the freshly deposited soil, then the presence of scent alone cannot orient termites or release dropping at specific sites. Bruinsma [11] sought to salvage the concept of cement pheromone by linking its volatility to the level of soil hydration, with more scent arising from wetter soil. But if a putative pheromone's volatility is tied to the wetness of soil, then it is simply an indicator for soil moisture. Wet soil has its own volatile component in the form of water vapour, and early studies of building in termites assumed a role for soil moisture and humidity in organizing mound expansion [20].

The claustral nature of the mound and nest serves to maintain a humid environment inside for both the termites and their symbiotic fungi [5]. Many termite species are vulnerable to desiccation, and forage below ground or construct soil envelopes around their food sources to shelter from environmental conditions [21]. Termites have been shown to sense humidity with their antennae [22] and cluster at zones of high humidity [23,24], suggesting that they may be able to sense a difference between the high humidity within their mounds and the lower humidity of the environment outside of them.

Turner [25] describes mound expansion as 'clearly tied to rainfall', when workers must remove water that percolates into the lower levels of the mound by bringing up and depositing soil that is far wetter than the soil of the surrounding mound surface [26]. The fact that termites are depositing wet soil as they build and capable of sensing the difference between the internal and external environments suggests the following broad hypothesis. Suppose that when environmental conditions are favourable, some cue characteristic of the internal environment such as elevated humidity extends as a 'bubble' past the mound edge into the outside world, dropping off to externally characteristic levels just beyond the physical boundary of the mound interior. And if termites with loads of moist soil are free to move to the outer surface of the mound within this protected zone and deposit soil without experiencing a rapid change in environmental conditions, depositing only when they reach the edge of the 'bubble', then that deposition of additional moist soil will move the boundary, allowing the 'inside' zone to progress further outward, in a feedback loop leading to the growth of the mound (figure 1).

There are many possible signals that could be sensed by termites, which would differ markedly if the termite were experiencing them inside the mound rather than outside of the mound. These include humidity, soil moisture, carbon dioxide levels and/or oxygen levels, temperature, colony odour, and the speed and turbulence of airflow. In this paper, we investigate humidity alone as a single candidate cue for this bubble mechanism, due to the importance of humidity to termites and the role of soil hydration in Bruinsma's [11] studies as outlined above.

Herein, we report internal mound humidity levels and characterize the humidity within and around an actively expanding build both under calm conditions and with induced external air flow. In order to reduce other potential environmental cues, we additionally perform laboratory experiments to quantify termite building activity in artificial environments that vary only in humidity level. By allowing workers to build inside chambers that vary predominantly in humidity level, we observe that *Macrotermes* termites translocate more soil and over a wider area under high humidity conditions.

2. Material and methods

(a) Humidity recording at mound breaches

Macrotermes maintain humidity in homeostasis to ensure the health of the termites and their mutualistic fungus gardens [6]. In order to characterize a baseline for humidity, we sampled three mounds of *Macrotermes michaelseni* (Sjostedt) (Blattoidea: Termitidae) in May 2017 at the Cheetah View Field Biology Station near Otjiwarongo, Namibia (20° 25′S, 17° 4′E). For each of the three mounds, a small breach in the outer surface of the mound was made by cutting directly into an internal conduit, 5 feet from the mound's base, or by cutting off the apex of the mound (figure 2*b*). Relative humidity was recorded at a depth of 15–20 cm within the conduit using Sensirion SHT75 temperature and humidity sensors placed at regular intervals along a rigid stick or linkage (accurate to 1.5% at steady-state conditions). Because the movement of the sensor can disrupt the humidity reading, we held the sensor steady and allowed a settling time of 10–15 s before storing values. Each sensor was sampled at a rate of roughly 0.25 Hz, for a minimum of 15 s (feasible sampling rate is highly dependent on the length of data transmission lines and the internal state of the sensor; one reading every 4 s is recommended by the manufacturer). For estimating humidity inside the mound, we used a ring support attached to the surface, which held a vertical linkage such that the central humidity sensor on the linkage was always at or near the physical mound boundary. The linkage could thus be used to sample inside the mound, at the mound surface, and external to the mound simultaneously. Where the angle of chimney or tunnel was such that the ring support could not be placed flush to the

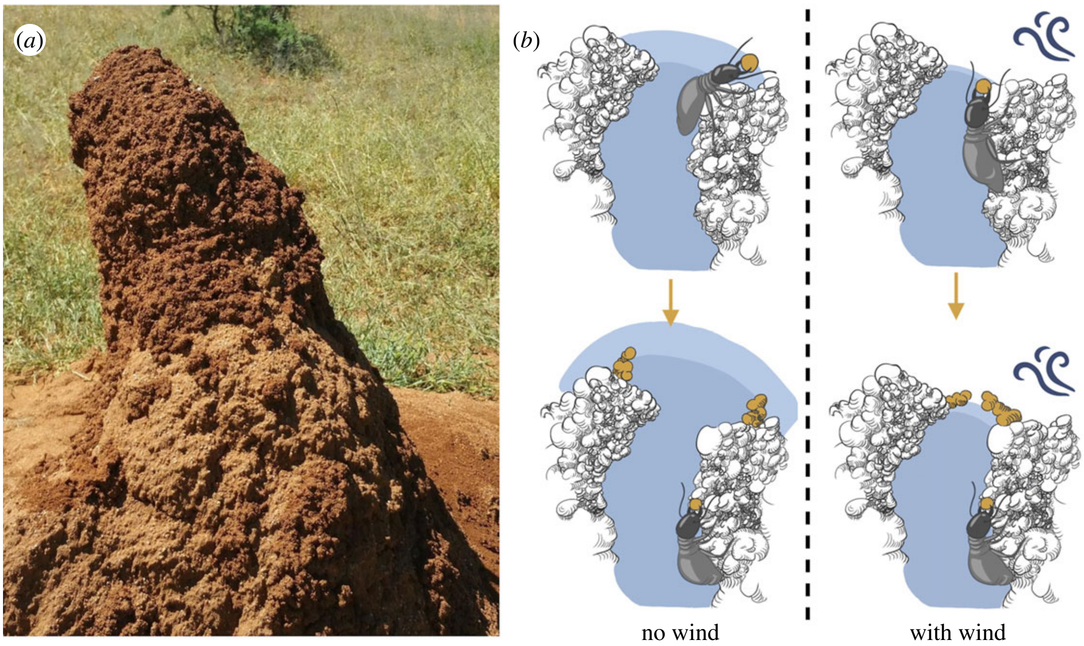

Figure 1. Mound expansion in *Macrotermes*. (*a*) A *Macrotermes michaelseni* mound with fresh deposition (dark, wet soil). Inset: A *M. michaelseni* worker. (*b*) Hypothesis for mound expansion via a humidity-guided template. A zone of high humidity exists inside the mound, supported by colony respiration and wet soil brought up from below ground for recent building; this zone extends slightly into the outside environment. Termites deposit soil at the boundary between high and low humidity. (left) The added soil extends the enclosed area, letting the 'bubble' of humid air advance, leading to mound growth. (right) When the spread of humidity outside is disrupted (e.g. by wind), soil is deposited at or below the tunnel mouth and closes it off. (Online version in colour.)

mound surface, the vertical linkage was extended as far as possible into the mound and the position photographed to allow *post hoc* position reconstruction.

(b) Humidity recording from active build sites

Worker termites translocate large amounts of water as they place parcels of wet soil at expanding build sites [26]. This creates a rapid drop in humidity between air close to the soil that is wetted to its plastic limit (approx. 25% water by weight) to aid in buildability and the drier ambient air outside the colony. In order to characterize the decrease in humidity around build sites, we recorded relative humidity at build sites with active termite workers on the mound surface. Actively expanding build on mounds takes the form of a series of crests and troughs (figure 2*a*), which collapse into each other in a reticulation sequence that leads to a sponge-like end product [27]. For estimating humidity during mound expansion, a minimum of two STH75 sensors were used (to ensure a reliable reading), placed close together on the end of a rigid stick. Humidity readings were taken from three locations on the expanding build of three mounds: 0.5 cm above the furthest extent of the expanding rim of a soil crest, at the level of the soil crest, and between crests, within a protected trough (figure 2*c*). In three trials for each of the same mounds above, the airflow of $0.8\ \mathrm{m\ s^{-1}}$ as measured by a handheld anemometer (Proster Trading LTD., PSTTL145US) was artificially applied, blowing laterally across the build site.

(c) Shielded and unshielded build sites

In order to create a protected environment around an expanding build site, three pairs of plastic cups were affixed to active building sites on three mounds of *M. michaelseni*. Any existing fresh depositions were scraped away, and the cups were placed over the holes exposed, held in place with a wire tent peg, and left for 12 h (figure 3*a*,*b*). One cup of each pair was left whole, while the other was perforated with a 1 cm hole in the top surface and a pair of 1 cm slits running around 80% of the cup's circumference, 1 cm from the base of the cup, to facilitate the escape of excess water vapour. The soil deposited was collected and air-dried. Dry masses were compared via an ANOVA test of two linear mixed models: a null model with only colony as a random effect and a model with treatment as a fixed effect and colony as a random one.

(d) Chamber with controlled humidity

In order to characterize whether the difference seen on the shielded and unshielded experiments can be explained by humidity alone, we devised in-lab experiments in which we used a feedback loop between a mist humidifier and humidity sensors to keep a set relative humidity inside an acrylic chamber (220 mm × 220 mm × 260 mm), (figure 4*d*). Inside this chamber, we placed a plastic cylinder packed with nest soil in its solid Atterberg liquid/plastic transitional state (approx. 25% water by weight) (ASTM Standard D 4318 test) capped off with an acrylic plate. The acrylic plate contained a 5 mm diameter hole in its centre, which supplied the only access by worker termites to the wet soil below, and a 3D-printed ring structure around it to confine termites placed on top of the acrylic plate. This set-up separates the construction process from the excavation process [18]. Consistently, termites tended to hide within moist soil. To do so within this setup, termites were obliged to transport the soil from the cylinder below onto the acrylic plate, and by measuring the weight of the plate before and after the experiments, we could know exactly how much soil the termites transported during the duration of the experiment.

We selected two different relative humidity settings for these experiments—a high setting of 80% relative humidity (RH) (measured during experiments at 81.3% ± 3.2% RH, $T = 26.79°\mathrm{C} \pm 0.37$), and a low setting of 40% RH (measured during experiments at 39.9 ± 5.2% RH, $T = 27.63°\mathrm{C} \pm 0.41$). For each treatment, we performed experiments on three different colonies, with three replicas per colony. For every colony, we extracted termites and soil from the respective mound, then termites were stored in a closed container lined with wet paper towels. For the cylinders, we sieved the soil through 1 mm mesh to remove large particulates, and for each colony soil cylinders were prepared together so that the soil water content was constant within same-colony experiments. At the beginning of each experiment, we weighed the plate, affixed it to a cylinder of soil, then placed 35 major workers on top and put it

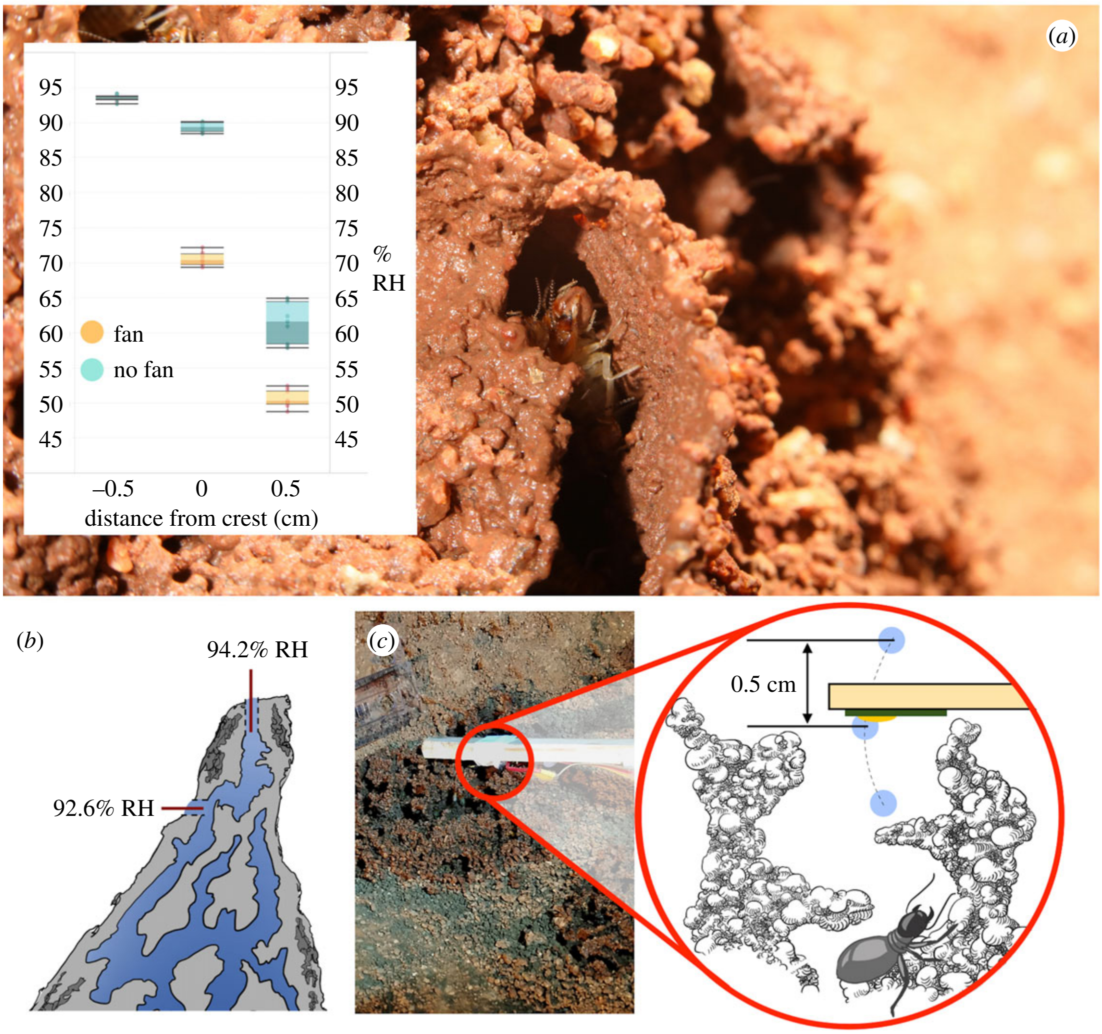

Figure 2. Measuring humidity *in situ* in the mound environment. (*a*) An active build site, showing the crests and troughs that form with expanding build. Inset: humidity readings around these structures, with and without a lateral external air flow applied. (*b*) A representation of a mound cross-section, showing the humidity of interior conduits, at the side and top of the mound. (*c*) Taking on-mound humidity measurements during active building, with diagrammatical zoom showing sensor locations (marked as dots) relative to crests of active build structure. (Online version in colour.)

in a humid or dry setting for 4 h. Once finished, we detached the mud cylinder from the plate, and removed any termites on the plate with forceps. We then placed all plates inside a food dehydrator, weighing them every 2 h as water evaporated. We recorded the dry mass after successive weight measurements of a plate showed an identical mass, indicating maximal water loss.

3. Results

(a) Humidity recording at mound breaches

Recordings from holes bored in the side of mounds showed an average relative humidity of 92.6% ± 0.44 (figure 2*b*) for the major internal conduits. Relative humidity was slightly higher for air near the apex of the mound, consistent with moist air being more buoyant (94.2% ± 0.29, figure 2*b*).

(b) Humidity recording from active build sites

In the absence of applied airflow, recordings from within the troughs between expanding crests of soil showed levels of humidity consistent with the internal mound conditions (93.48 ± 0.4, figure 2*a* inset). The elevated relative humidity extended beyond the rim of the growing crests of wet soil deposited by workers (89.4 ± 0.63), but at 0.5 cm above the expanding build, the humidity had plummeted to almost ambient conditions (61.47 ± 2.83, figure 2*a*, inset). When air flow was applied to the expanding build, the humidity measure in the protected troughs remained unchanged (93.38 ± 0.28), but levels recorded at the rim of the exposed crests dropped rapidly (70.55 ± 0.94), while recordings at 0.5 cm above the expanding build were similar to environmental conditions outside the mound (50.56 ± 1.22).

(c) Shielded and unshielded build sites

Analysis of the mass of soil deposited in the plastic cups showed that termites had a larger amount of nest expansion/activity in the shielded cups (77.27 g ± 11.57) when compared to the unshielded ones (41.19 g ± 14.79) (figure 3*d*). The parameters and results of a linear mixed model comparing soil mass against cup treatment, with colony as a random effect, are shown in table 1, demonstrating that the difference in mass deposition is significant even when colony variance is taken into account.

(d) Chamber with controlled humidity

Lastly, we observed a similar trend to the shielded experiments in our laboratory ones. Experiments performed in the high ambient humidity treatment displaced more mass (6.83 g ±

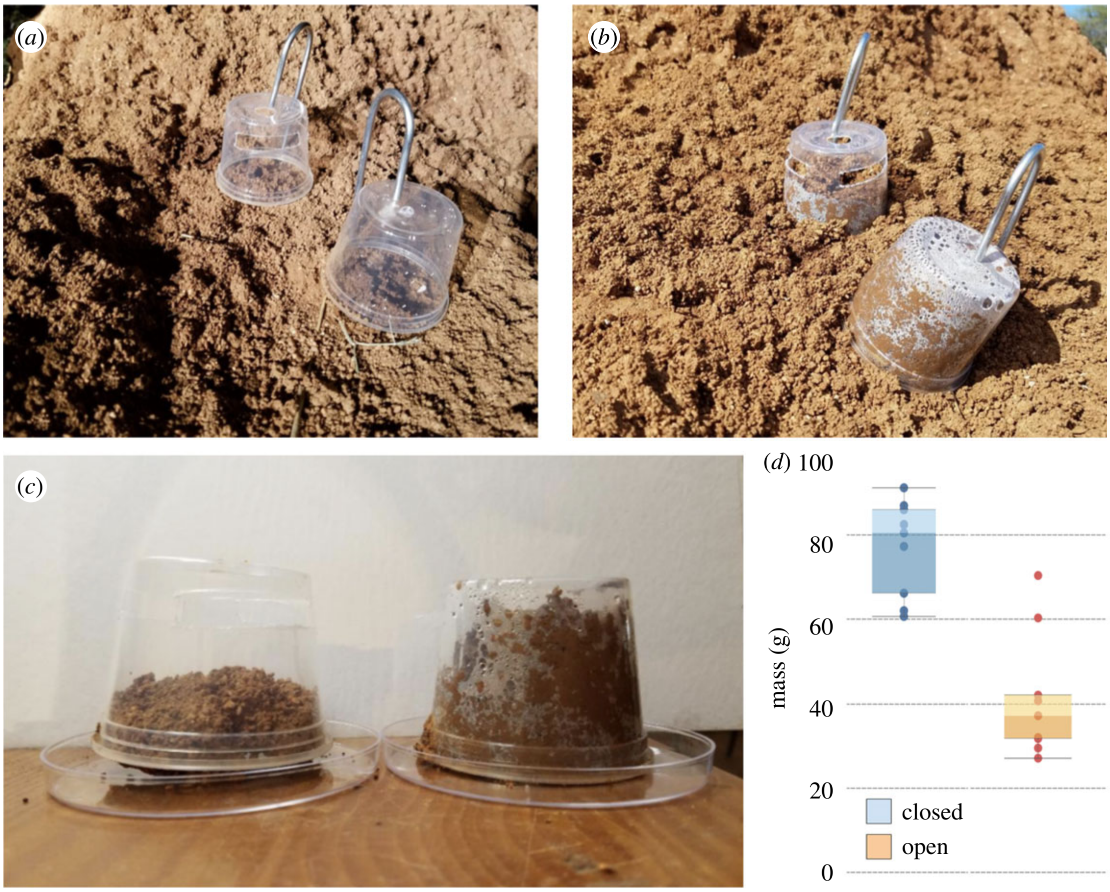

Figure 3. Soil transport in shielded and unshielded build sites. Plastic cups were affixed to active building sites on *M. michaelseni* mounds. Any existing fresh depositions were scraped away, and the cups were placed over the holes exposed, held in place with a wire tent peg, and left for 12 h. (*a*) Unshielded (left) and shielded (right) cups placed over active build sites on a *M. michaelseni* mound. (*b*) Cups *in situ* after 12 h of overnight building activity. (*c*) Unshielded (left) and shielded (right) cups post-experiment, preparing for weighing. (*d*) Comparing the dry mass of unshielded (left) and shielded (right) soil transported by *M. michaelseni* into the cups over a 12 h period ($n = 9$, 3 colonies, 3 experiments per colony). (Online version in colour.)

2.76) than the ones performed in low ambient humidity (4.86 g ± 1.66) (figure 4*e*). We observed large colony-level variability in the measured mass (electronic supplementary material, figure S1), but a linear mixed model comparison testing colony as a random effect (table 2) still showed a significant difference in the mass displacement between the two treatments ($p < 0.01$) [28]. The area of the plate covered by soil and the volumetric envelope (reconstructed using the 3D point cloud from the active depth sensor [24]) were also significantly different between treatments ($p < 0.01$, figure 4*e*), though these are correlated with mass and may not represent qualitative differences in structure.

4. Discussion

Our results suggest that termites will expand their new building into areas of higher relative humidity, while low relative humidity environments may inhibit mound expansion. When a 'bubble' extending internal atmosphere beyond the surface of the mound was artificially created by shielding active build sites, termites translocated significantly more soil. While many parameters could have been responsible for this increase, our laboratory experiments showed that changes in relative humidity are sufficient to produce this behaviour. Humidity recordings from the surface of expanding mound sites showed the presence of a zone of high humidity extending beyond the surface of the mound. This zone was highly dependent on ambient conditions around the mound, being easily disrupted by increasing air flow over the build site.

The template for mound expansion is formed by the extension of the internal mound atmosphere beyond the soil structure of the mound. Termites are not just attracted to wet spots in a manner akin to previous models of scent labelling. Simply searching for the wettest places at an active build site would be problematic because, due to gravity and evaporative effects, sometimes the base of crests and pillars can be wetter than the rims.

Instead, the natural convection of buoyant humid air upward and away from the mound [23] extends the high humidity of the mound's interior a short distance beyond the solid structure of the mound soil, and allows termites to move to the edges of the growing build within what has been described as a 'viscous boundary layer' [23], without being subjected to drier and more turbulent conditions outside the mound. This movement of nest-level humidity beyond the confines of the conduits inside the mound is reinforced as each new deposition of wet soil elevates the humidity around construction sites. The workers are effectively chasing a moving front of humid air that expands with the build. In the on-mound experiments, termite workers could be seen to regularly sample the air past the structure of the mound with their antennae (electronic supplementary material, video S1). The extension of high humidity beyond the substrate of the mound may allow workers to move to the furthest extent of construction sites to expand the build, while the infiltration of

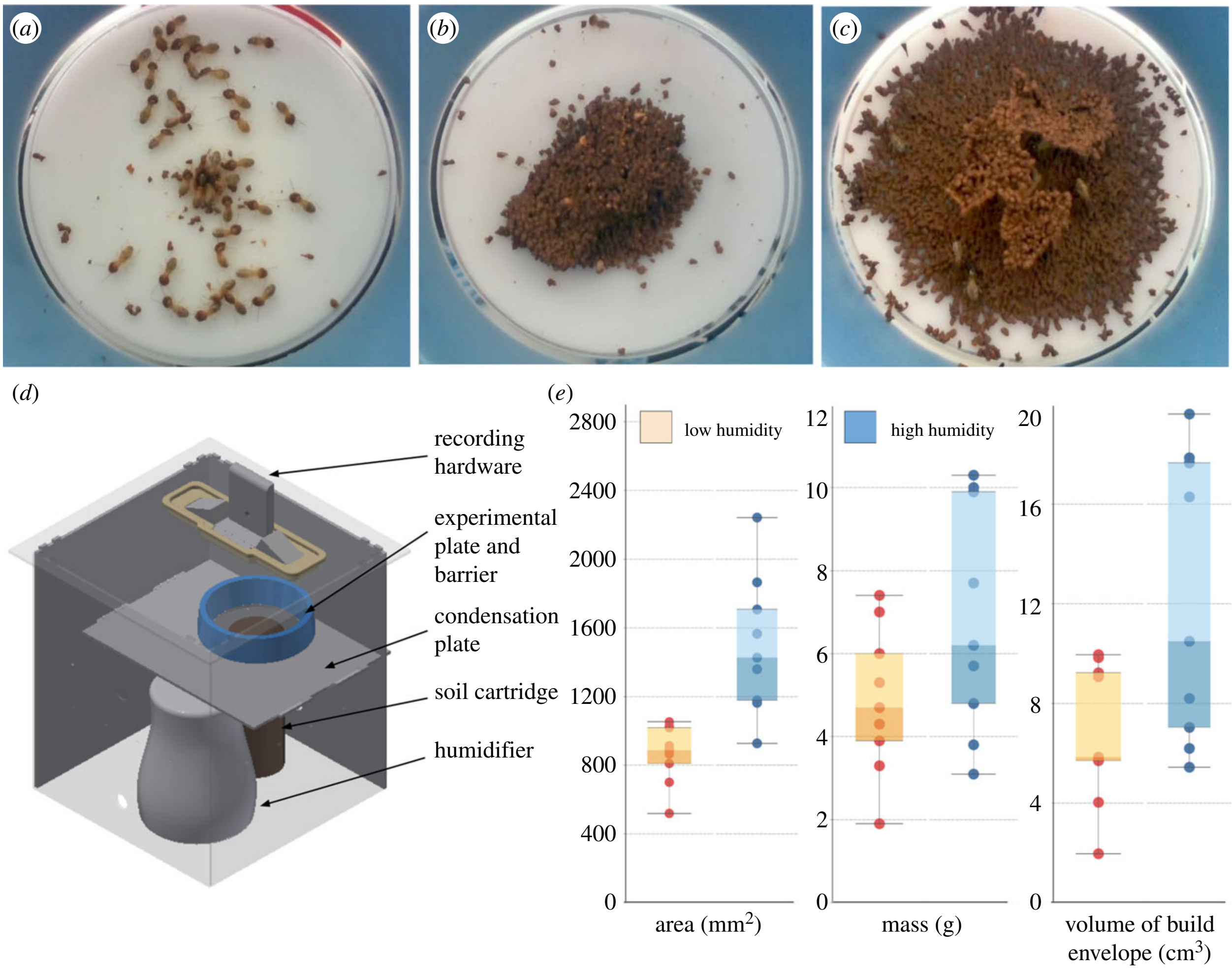

Figure 4. *M. michaelseni* construction in a humidity-controlled environment. Termite workers on a flat plate were given a packed soil reservoir with a single access point, and allowed to build for 4 h at either high (80%, $T = 26.79°\mathrm{C} \pm 0.37$) or low (40%, $T = 27.63°\mathrm{C} \pm 0.41$) ambient humidity. The resulting structures were completely dried, then weighed. (*a*) Build plate at the start of an experiment. (*b*) Build plate after 4 h of low-humidity building. (*c*) Build plate after 4 h of high-humidity building. (*d*) The experimental setup. Image from Carey *et al*. [24], showing the humidity-controlled chamber (220 mm × 220 mm × 260 mm), build plate, and barrier ring which prevents workers leaving the plate and also shields the plate from air currents, placement of the humidifier used to hold humidity constant, and the packed soil cartridge used as a soil reservoir by the termites. The build plate was shielded from direct air droplets expelled from the humidifier by a condensation plate placed above the humidifier (146 mm from the base of the chamber). (*e*) Boxplots of the three different measurements (area of the plate covered by soil, dry mass, and volume of build envelope) under low humidity (left) and high humidity (right) conditions, where boundaries show quartiles; whiskers show 1.5 × interquartile range. All three properties showed meaningful differences between each other (linear mixed model, table 1, electronic supplementary material, table SI1 and table SI2). (Online version in colour.)

Table 1. Linear mixed model results for dry soil mass deposited inside the cups as a function of shielding status, 18 observations, 3 replicas in 3 different colonies for 2 different treatments, d.f. = 4 marginal R^2/conditional R^2 0.687/0.687.

fixed effect	dry mass	CI	*p*-value
intercept	41.23	33.07–49.40	<0.0001
shielded	35.98	24.43–47.52	<0.0001
random effect			**s.d.**
colony			0.0009

Table 2. Linear mixed model results for dry soil mass deposited on the plate surface as a function of humidity. 19 observations, 3 replicas in 3 different colonies for 2 different treatments, d.f. = 4, marginal R^2/conditional R^2 0.142/0.790.

fixed effect	dry mass	CI	*p*-value
intercept	3.73	1.26–6.20	<0.01
humidity	0.04	0.02–0.06	<0.01
random effect			**s.d.**
colony			1.84

low-humidity air (e.g. driven by wind outside) would restrict their movement and cause them to drop their loads of soil before reaching the outside of the build structure, closing off the build site.

Humidity was identified early in the study of termite mounds as an important factor governing termite behaviour [20], with termites responding to dry air by building in a manner that maintains the homeostasis of a high-humidity internal environment. Later work [29] challenged this interpretation, finding that construction was not triggered by dry air. Rather the rate of construction went down as humidity decreased. These findings can be reconciled if humidity is not a trigger that leads termites to drop soil parcels when it drops below some threshold, but a traffic signal, a dead end to their movement path as they move from internal mound conditions to the less hospitable external environment. The organizational value of a path's end as a trigger to perform a behaviour has been explored in termite tunnel excavation, where digging must occur at the end of tunnels in order to efficiently extend them through soil and termites generally move down the tunnels until their paths are blocked by a wall or a queue of other termites waiting to dig [30].

Macrotermes workers, travelling to build sites along recruitment paths labelled with trail pheromone [11,31], moving to the periphery of the build site guided by their own internal path integration [32] or guided by the topography of internal conduits, may perceive a sudden drop in humidity as a barrier to further movement and search for a place to deposit their loads of soil. The terminal stimulus governing where to drop soil could be encountering the steep drop in relative humidity. Within a mound, by contrast, where humidity is high everywhere and no such transitions are expected, other cues must govern remodelling. Soil translocation in subterranean termites has been suggested to be governed by tactile cues and the crowding of individuals, which block movement in tunnels [30]. Inside *Macrotermes* mounds, where humidity is high, the mechanics of soil translocation may be similar to tunnelling in subterranean termites. A scheme that unifies a putative humidity template with the mechanics of tunnelling would involve termites responding to environmental conditions that inhibit movement, effectively blocking their path as they are reluctant to leave the high humidity of the mound, by seeking locally for tactile cues that guide the placement of soil. Tactile information from surface irregularities such as small metal balls [11], and topographical features such as lumps [18] and concave depressions [19], have been shown to be sufficient to trigger dropping behaviour during building, but cannot attract termites from beyond tactile range. Combining a humidity template with a tactile system would provide a means for getting workers to the edge of expanding construction and provide foci for where to deposit once there.

The ability to maintain a zone of humid air and expand the mound may be governed by the volume of wet soil being moved up from deeper in the nest and the recruitment to build sites. This would explain why construction in the wet season expands the mound, while a breach in the mound in dryer months is often simply plugged flush with the mound's outer surface. Wet soil is moved up from deep in the mound, potentially raising the humidity wherever in the mound this soil is deposited [25]. This local elevation in humidity within the mound, in proximity to build sites, would help to support the extension of internal mound humidity beyond the outer surface of the mound. In the dry season, there would be no elevation of humidity at the site of breaches. Our findings also suggest that mound expansion is more likely to occur when the air around mounds is calm and the ambient humidity is high. We simulated the manner in which environmental conditions disrupt the zone of humidity around build sites with applied airflow from a fan, but under natural conditions this disruption would occur not only with increased wind, but also with a drop in ambient humidity or the drying effect of the sun and elevated temperature. The building could also shut down if the recruitment of new or continuing builders slowed down and allowed evaporation of water from the soil at build sites to outpace incoming water from new deposition.

The role of humidity in organizing construction in *Macrotermes* may have arisen from the requirement for termites to be responsive to the humidity needs of the symbiotic fungus they rear in gardens [33]. The fungus requires a narrow range of humidity in order to thrive, and produces water vapour as a metabolic waste [34]. Humidity as a signal that organizes labour may allow communication between the fungi and their termite gardeners through the medium of soil moisture and humidity. It remains to be determined if termites in families other than the fungus-gardening Macrotermitinae make use of humidity as a template for construction, but the fact that Attine (leaf cutting) ants respond to dry airflow and have independently evolved mutualistic fungal gardening [35] suggests that the requirements of this common lifestyle may be more important than the phylogenetic relationship.

Data accessibility. Data are available from the Dryad Data Repository: https://doi.org/10.5061/dryad.xd2547ddr [36].

Authors' contributions. Study concept: P.B., D.S.C., N.C., R.S., S.T., R.N., J.W.; study design: P.B., D.S.C., N.C., J.W.; field/laboratory work: P.B., D.S.C., N.C.; data analysis: D.S.C.; interpretation: P.B., D.S.C., N.C., J.W.; writing: P.B., D.S.C., N.C., J.W. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. The research reported in this publication was supported by the National Institute of General Medical Sciences of the National Institutes of Health under award number R01GM112633. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.

Acknowledgements. We thank the Harvard Institute for Quantitative Social Science for consultation on statistical methodology, and the Cheetah Conservation Fund for providing research facilities.

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