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Termite mounds harness diurnal temperature oscillations for ventilation

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Many species of millimetric fungus-harvesting termites collectively build uninhabited, massive mound structures enclosing a network of broad tunnels that protrude from the ground meters above their subterranean nests. It is widely accepted that the purpose of these mounds is to give the colony a controlled microclimate in which to raise fungus and brood by managing heat, humidity, and respiratory gas exchange. Although different hypotheses such as steady and fluctuating external wind and internal metabolic heating have been proposed for ventilating the mound, the absence of direct in situ measurement of internal air flows has precluded a definitive mechanism for this critical physiological function. By measuring diurnal variations in flow through the surface conduits of the mounds of the species Odontotermes obesus, we show that a simple combination of geometry, heterogeneous thermal mass, and porosity allows the mounds to use diurnal ambient temperature oscillations for ventilation. In particular, the thin outer flutelike conduits heat up rapidly during the day relative to the deeper chimneys, pushing air up the flutes and down the chimney in a closed convection cell, with the converse situation at night. These cyclic flows in the mound flush out CO2 from the nest and ventilate the colony, in an unusual example of deriving useful work from thermal oscillations.

Significance

Termite mounds are meter-sized structures built by millimeter-sized insects. These structures provide climate-controlled microhabitats that buffer the organisms from strong environmental fluctuations and allow them to exchange energy, information, and matter with the outside world. By directly measuring the flow inside a mound, we show that diurnal temperature oscillations drive cyclic flows that flush out CO2 from the nest and ventilate the mound. This swarm-built architecture demonstrates how work can be derived from the fluctuations of an intensive environmental parameter, and might serve as an inspiration and model for the design of passive, sustainable human architecture.

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significant bulk flow across the wall, effectively ruling out wind as the primary driving source.

Within the mound, a range of indirect measurements of CO$_2$ concentration, local temperature, condensation, and tracer gas pulse chase (8–10, 11, 14) show the presence of transport and mixing. However, a complete understanding of the driving mechanism behind these processes requires direct measurements of flow inside the mound. This is difficult for several reasons. First, the mound is opaque, so that any instrument must be at least partly intrusive. Second, expected flows are small (centimeters per second), outside the operating range of commercial sensors, requiring a custom-engineered device. Third, because conduits are vertical, devices relying on heat dissipation, or larger, high heat capacity setups can generate their own buoyancy-driven (and geometry dependent) flows, making measurements ambiguous (15). Finally, and most importantly, the mound environment is hostile and dynamic. Termites tend to attack and deposit sticky construction material on any foreign object, often within 10 min of entry. If one inserts a sensor even briefly, termites continue construction for hours, effectively changing the geometry and hence the flow in the vicinity of the sensor.

To measure airflow directly, we designed and built a directional flow sensor composed of three linearly arranged glass bead thermistors, exposed to the air (SI Appendix). A brief pulse of current through the center bead creates a tiny bolus of warm air, which diffuses outward and is measured in either neighboring bead. (The operating mechanism is similar in principle to that of ref. 16.) Directional flow along the axis of the beads biases this diffusion, and is quantified by the ratio of the maximum response on each bead, measured as a temperature-dependent resistance. In a roughly conduit-sized vertical tube, this resistance–change metric depends linearly on flow velocity, with a slight upward bias due to thermal buoyancy. This allows us to measure both flow speed and direction locally. The symmetry of the probe allows for independent calibration and measurement in two orientations by rotating by 180° (arbitrarily labeled upward and downward; SI Appendix).

In live mounds, the sensor was placed in a surface conduit at the base of a flute for $\leq 5$ min at a time to avoid termite attacks, which damage the sensors. For a self-check, the sensor was rotated in place, such that a given reading could be compared on both upward and downward calibration curves. We also measured the flow inside an abandoned (dead), unweathered mound that provided an opportunity for long-term monitoring without having termites damage the sensors. Simultaneous complementary measurements of temperature in flutes and the center were taken. To measure the concentrations of CO$_2$, a metabolic product, a tube was inserted into the nest; in one mound in the center slightly below ground and another in the chimney at $\approx 1.5$ m above. Gas concentration measurements were made every 15 min by drawing a small volume of air through an optical sensor from the two locations for most of one uninterrupted 24-h cycle.

Nearly all of the 25 mounds that were instrumented were in a forest with little direct sunlight. In Fig. 2A, we show flow measurements in 78 individual flutes of these mounds as a function of time of day. We see a clear trend of slight upward (positive) flow in the flutes during the day, and significant downward (negative) flow at night. The data saturates for many night values, as the flow speed was larger than our range of reliable calibration (SI Appendix). In Fig. 2B, we show the flow rate for a sample flute in the abandoned mound. Notably, it follows the same trend seen in live mounds, but the flow speeds at night are not nearly as large as for the live mounds. For both live and dead mounds, we also show the
facilitating transport of respiratory gases. Observations of the well connectedness of the mound and the impermeability of the external walls imply that flow in the center of the mound, to obey continuity, must move in the vertical direction opposite that of the flutes. When the flutes are warmer than the interior, air flows up in the flutes, pushing down cooler air in the chimney. The opposite occurs when the gradient is reversed at night (Fig. 3). The air flowing down the flutes is significantly warmer than ambient temperature, a situation only possible if it were being pushed by even warmer air flowing up the chimney.

This model predicts flow speeds comparable to those observed in the mound (SI Appendix), and is consistent with the quick uptake and gradual decline of CO$_2$ measured in the chimney: with the evening temperature inversion, convection begins to push rich nest air up the chimney before diffusion across the surface gradually releases CO$_2$ from the increasingly mixed mound air. (See Movie S1 for a sequence of thermal images of the inversion that accompanies this drop.) This forcing mechanism is inherently transient; if the system ever came to equilibrium and the gradient disappeared, ventilation would stop.

It has long been thought that animal-built structures, spectacularly exemplified by termite mounds, maintain homeostatic microhabitats that allow for exchange of matter and energy with the external environment and buffer against strong external fluctuations. Our study quantifies this by showing how a collectively built termite mound harnesses natural temperature oscillations to facilitate collective respiration. The radiatorlike architecture of the structure facilitates a large thermal gradient between the insulated chimney and exposed flutes. The mound harnesses this gradient by creating a closed flow circuit that straddles it, promoting circulation, and flushing the nest of CO$_2$. Although our data comes entirely from one termite species, the transport mechanism described here is very generic and is likely dominant in similarly massive mounds with no exterior holes that are found around the globe in a range of climates. A natural question that our study raises is that of the rules that lead to decentralized construction of a reliably functioning mound. Although the insect behavior that leads to construction of these mounds is not well understood, it is likely that feedback cues are important. The knowledge of the internal airflow rates and transport mechanisms might allow us to get a window into these feedbacks and thus serve as a step toward understanding mound morphogenesis and collective decision making. The swarm-built structure described here demonstrates how work can be derived, through architecture, from the fluctuations of an intensive environmental parameter—a qualitatively different strategy than that of most human engineering that typically (18) extracts work from unidirectional flow of heat or matter. Perhaps this might serve to inspire the design of similarly passive, sustainable human architecture (19, 20).

**Experimental Procedures**

**Steady Flow Measurement.** In an area within walking distance of the campus of National Centre for Biological Sciences Bangalore, India, 25 mounds were chosen that appeared sufficiently developed ($> 1$ m tall) and intact. All mounds were located in at least partial shade, but received direct sunlight intermittently during the day. Direct sunlight does not appear to play a direct role in the flow schedule (SI Appendix). Full exposure would lead to orientational dependence of temperature and air flows.) The scatter plot of steady flow (Fig. 2A) represents individual measurements of the flow in the large conduits found at the end of each available flute.

To place the probe, a hole was manually cut with a hole saw fixed to a steel rod, usually to a depth of about 1–3 cm before breaking into the conduit. With a finger, the appropriate positioning and orientation of the sensor was determined. Occasionally, the cavity was considered too narrow ($< 3$ cm diameter), or the hole entered with an inappropriate angle, in which case it was sealed with putty and another attempt was made.

Because internal reconstruction, involving many termites and wet mud, continues long after any hole is made, the same flute was never measured...
twice. In a round of measurements, flows in 1–3 (out of approximately 7 available) flutes of each of ~8 nearby mounds were measured, a process which took several hours. Each of the 25 mounds was visited 2–3 times to use unmeasured flutes, but deliberately at different times of day to avoid possible correlations between mound location and flow pattern.

An individual measurement of flow was taken for ~2 min in each orientation, such that the response curves from which the metric and then flow are calculated are averaged over many pulses (~6 pulses per min). The error bar of each constant flow velocity measurement in Fig. 2A indicates the deviation in measured flow between orientations. Care was taken to ensure that the probe temperature remained close to the interior flute temperature, and no long-term drift in measured velocity was observed as the probe equilibrated. Periodically between measurements, the sensor was tested in the same apparatus to check that it remained calibrated, especially when thermistors were damaged or dirtied by termites and needed to be cleaned.

The dead mound referenced in the text was identified as such because no repairs were made upon cutting holes for the sensor. As it was also intact (there were no signs that erosion had yet exposed any of the interior cavities) and within reach of electricity, it was possible to make continuous flow measurements that could be compared with the brief measurements for live mounds.

**Geometry and Sources of Error in Flow Measurement.** In situ measurements take place in a complex geometry, and the width, shape, and surrounding features can be highly variable. This can lead to significant variation in local velocities, even causing some local velocities to go against the average trend; this is a generic feature of flow through disordered, porous media (21, 22). In addition, the width, shape, and impedance of a channel are different from our calibration setup, and the position of the probe within a channel could not be exactly known. These factors are most likely the dominant source of error for any given measurement in the field, either over- or underestimating the flow in a particular conduit. This error, though potentially as large as a factor of ~2, is reflective of the natural variation in mound geometry, is not correlated to any other parameter, and cannot mistake the direction of flow, such that the trend in average flow remains unambiguous.

**Temperature Measurements.** Temperatures in the dead mound reported in Fig. 2B in the main text were obtained by implanting iButtons (DS1921G; Maxim) into the mound using the hole saw and closing the openings with wet mud. Two iButtons were placed in flutes at the same location where flow data had been acquired. Another two iButtons were placed 5–10 cm below the surface, in the nooks between flutes, such that they were located roughly in the periphery of the central chimney. As shown in Fig. 2, the temperature from the measured flute minus the average temperature measured by the centrally placed iButtons. The raw data were slightly smoothed before taking the difference, to reduce distracting jumps in data from the iButtons, which have a thermal resolution of 0.5 °C.

In the large healthy mound, digital temperature/humidity sensors (SHT11; Sensiron) were implanted at different heights near the central axis. Screened windows protected the sensors from direct contact by termites and building material, and remain coupled to the interior environment. The sensors and Arduino were powered with a high capacity 12-V lead acid battery and they recorded temperature for approximately two days. The iButtons were placed in the bases of flutes in four sides of the same mound. Temperature differences reported in Fig. 2A were calculated from the average of flute temperatures and central axis temperature at the corresponding height.

Moreover, there is not much of a dependence of the temperature along the center of the mound on cardinal direction, as seen in Fig. 4, consistent with the fact that these mounds are not directly heated by the sun. Finally, we note that the temperature differences between interior and flutes shown in Fig. 1 are significantly larger at night than during the day. This, and/or the vertical asymmetry of the convective cell (in that the flutes are closer to the top of the convective cell) might be responsible for the observed asymmetry in flow magnitudes between night and day.

**Permeability and Diffusibility.** A hollow, conical sample of a flute was cut from a mound. The bottom was sealed with gypsum, such that the pores in the wall material and length of plastic tubing are the only path in and out of the cone.

Air was pulled by a vacuum pump from the tube through the volumetric flow meter. The pressure differential between inside and outside of the cone was measured by the displacement of water in a column between the cone and flow meter. Fig. 5, Left shows the 20-cm-tall conical sample and Right Top relationship between back pressure and average flow. From this graph, one can read the local flow induced across the mound wall due to a pressure differential from incident wind. Wind in the area during the study was typically in the range 0–5 m/s, which could produce a maximum dynamic pressure \( P = \frac{1}{2} \rho V^2 \approx 0–15 \text{ Pa} \), giving a maximum flow through the surface of 0.01 mm/s. With even the most liberal approximations, this is not enough to produce bulk flow of the order we measured, in agreement with the observed negligibly small transient flows in tests with a powerful fan. If macroscopic holes penetrated the mound surface in some locations, they would dramatically change the permeability estimate of the mound as a whole. However, such holes were not observed in these mounds, and the species seems to fill in even the smallest holes. This behavior contrasts that of other species, which appear to tolerate some holes; O. obesus actively closed narrow holes made for the CO₂ measurement, and we have observed that Macrotermes michaelseni in Namibia did not.

Impermeability to bulk flow of the wall does not mean nonporous or impermeable to diffusion. Cooking gas was injected into the conical sample and measured by combustible gas sensor that was sealed inside the conical sample. Fig. 5, Right Bottom shows that it diffuses out the surface over the course of about 2 h (following close to exponential decay).

**CO₂ Measurements.** One large (~2 m tall), apparently healthy mound was chosen (that shown in Figs. 1 A and B and 3; Movie S1) for measurements. One hole was drilled from ground level diagonally down into the nest and another into the central chimney 1.5 m above ground. Then 1/4 inch tubing was inserted in the holes and left overnight such that the termites sealed the holes at the surface of the tubes snugly in place, and flow from the whole range IR LED CO₂ sensor was fitted with a custom machined, air-tight cap with two nozzles, such that air pulled into the cap would gradually diffuse across the sensor membrane and the response could be recorded with an Arduino onto a laptop computer. For most of one 24-h cycle, every 15 min air was drawn from each of the tubes in the mound through the sensor with a 50-ml syringe, pulling gradually until the response leveled out, meaning the full concentration of mound air had diffused across the sensor membrane. When termites periodically sealed the end of the tube inside the mound, a few milliliters of water was forced into the tube, softening and breaking the seal so measurements could continue.
Prediction of Mean Flow Speed. As a model for a convective circuit within a termite mound, we choose a pipe radius \( r \), in the shape of a closed vertical loop of height \( h \), where the temperature difference between left and right side of the loop is \( \Delta T \). The total driving pressure is \( \rho A \Delta T g h \), where \( \rho \) is air density and \( A \) is the coefficient of thermal expansion, and Poiseuille’s law gives

\[
Q = \frac{\rho A \Delta T g h}{8 \eta h} \cdot \frac{x^4}{x^2 + 2}
\]

[1]

where the factor of 2 comes from the resistance on both sides of the loop. Calculating flow speed:

\[
V = \frac{Q}{\pi r^2} = \frac{\rho A \Delta T g r^2}{16 \mu}
\]

[2]