# *Insects as Architects*
# *How insects engineer their ecosystems*

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# *The short history of human architecture*

**Cairn de Barnenez (ca. 4850 BC)**

**Lower Manhattan. One World Trade Center, the tallest skyscraper in the Western Hemisphere (ca. 2016 AD)**

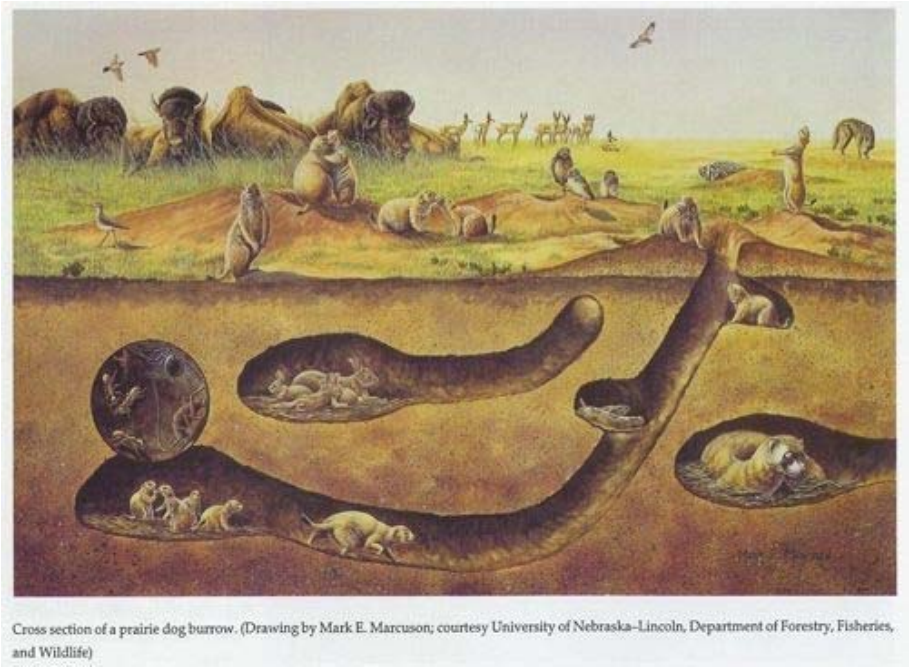
http://www.ancient-origins.net/ancient-places-europe/cairn-de-barnenez-one-oldest-structures-world-005771

https://en.wikipedia.org/wiki/Manhattan

# *Animals are architects too*

## Including Mammals…….

***Beaver dam, somewhere near Alberta, Canada***

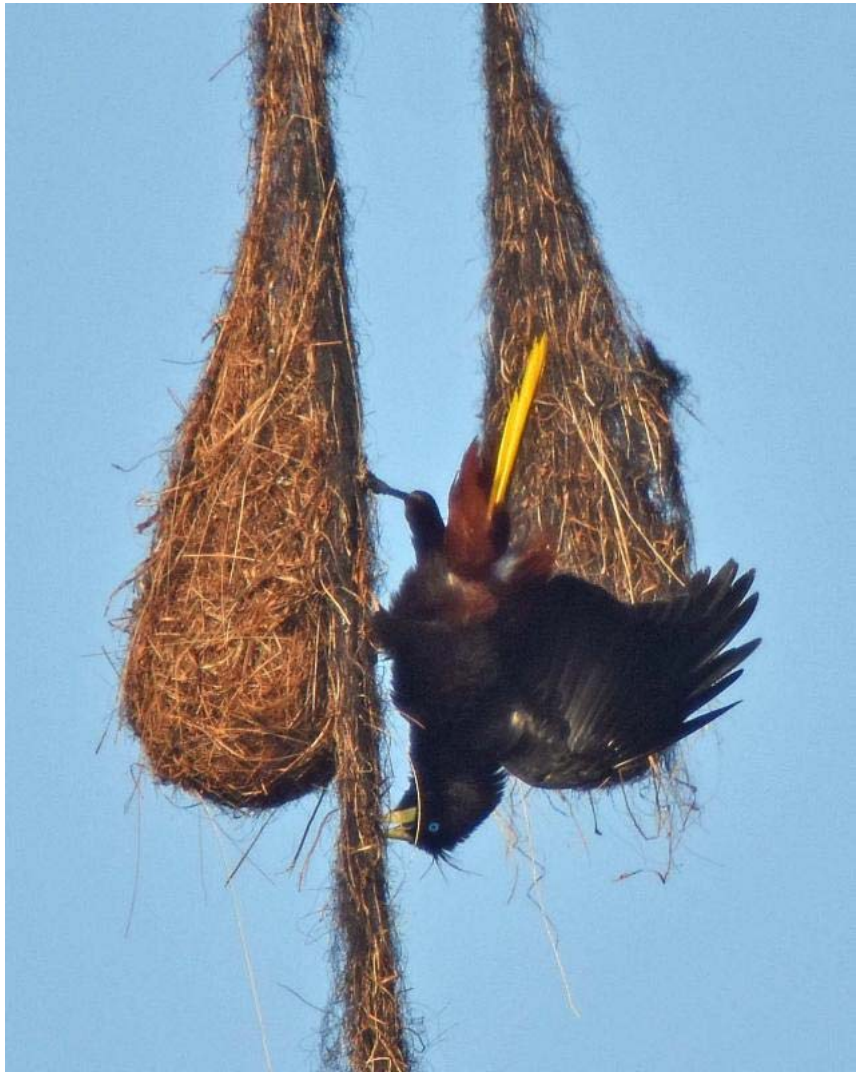


Cross section of a prairie dog burrow. (Drawing by Mark E. Marcuson; courtesy University of Nebraska–Lincoln, Department of Forestry, Fisheries, and Wildlife)

***Prairie dog nest architecture***

# ……birds…..

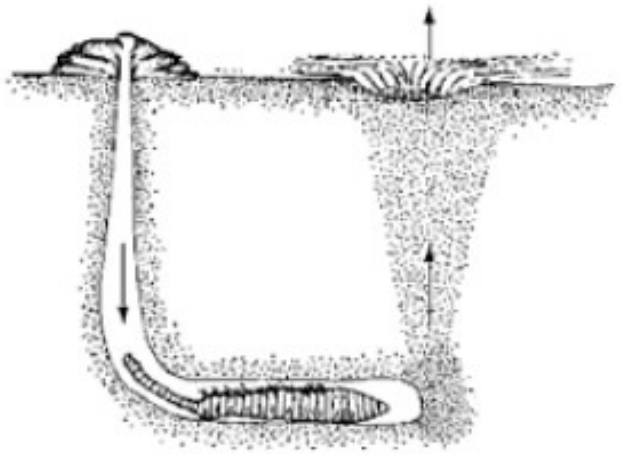
***Baya weaverbird***
***(South Asia including India)***



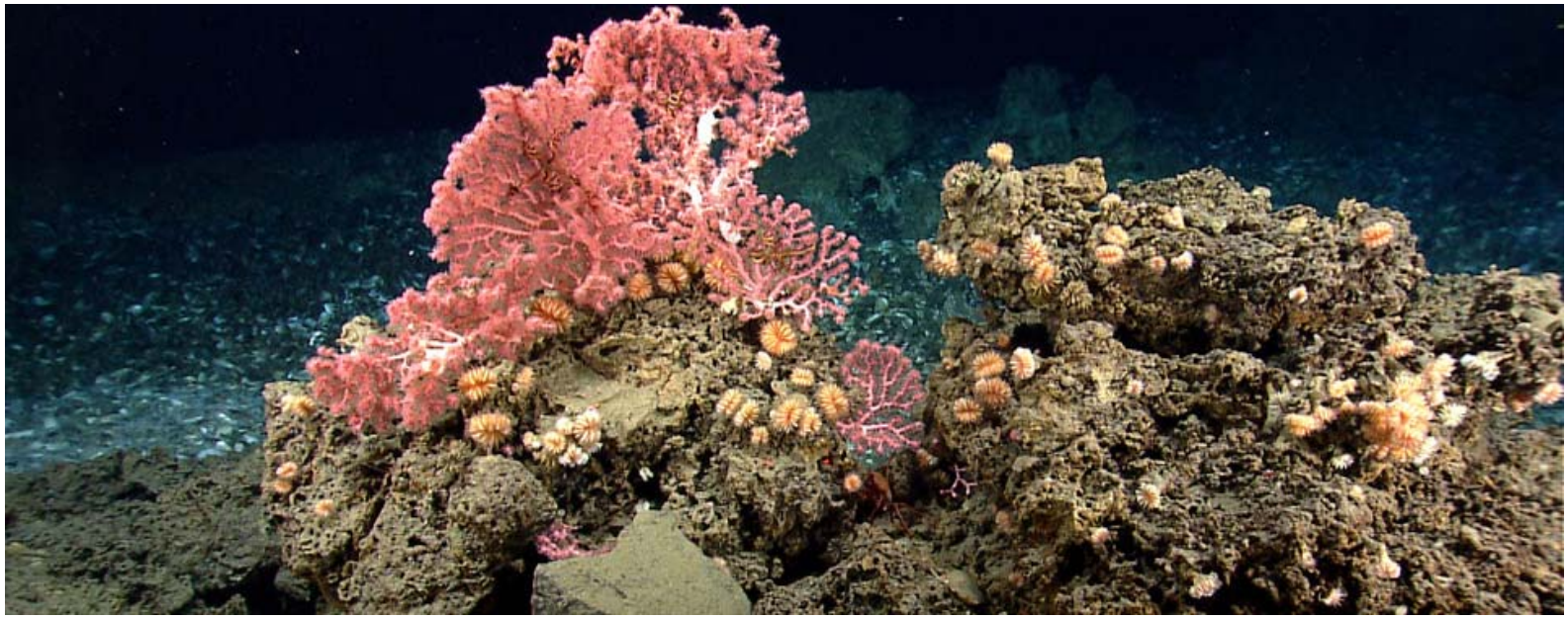
***Oropendola***
***(South America)***

# …and marine animals….

***Lugworm (Arenicola Spp.)***



***Coral Reef (mixed species)***



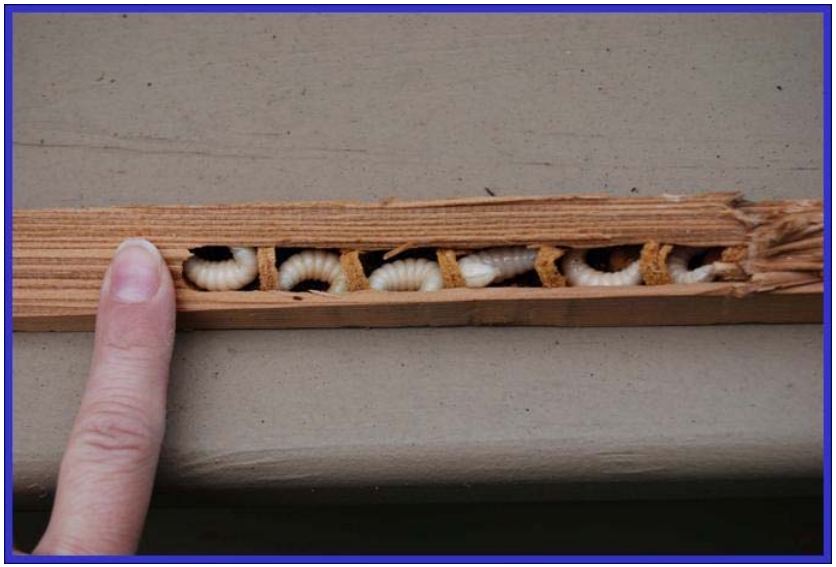
# *Insect architecture is everywhere*

***Rock Bee (Apis Dorsata)***

***Weaver ant (Oecophyliia spp.)***


**Paper wasp (Polistes major major)**

***Carpenter Bee (Xylocopa Spp.)***

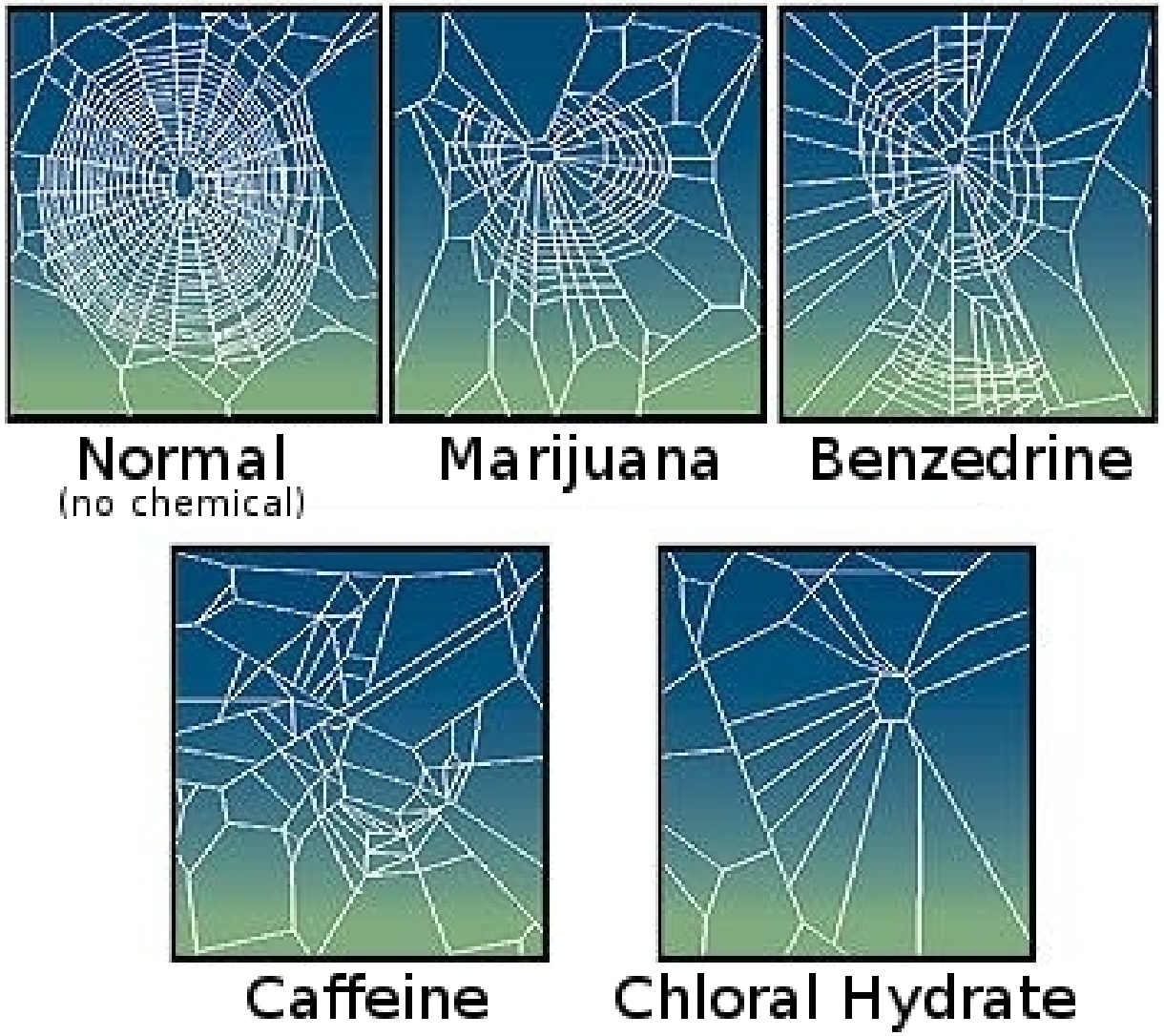


# *Potter wasps building nests*

https://www.youtube.com/watch?v=t6lEGs9M3sY

# *Spider webs are marvels of design and material strength*

# …and require tremendous coordination in space and time (which can be experimentally disrupted!)




*Noever, R., J. Cronise, and R. A. Relwani. 1995. Using spider-web patterns to determine toxicity. NASA Tech Briefs 19(4):82.* ***(From New Scientist magazine, 29 April 1995)***

# *What are termite mounds?*

- Large scale colonies of termites
- Varying shapes and sizes, but similar structures
- Each contains a colony extending up to a few meters over and under ground.
- Colony contains a queen, soldiers, major and minor workers and alates.
- Termites farm fungus to help digest cellulose.
- Complex maze of tunnels and bridges inside the mound

# *While the city sleeps…..*

# *Termites are eusocial mound building cockroaches*

Mound

Alates

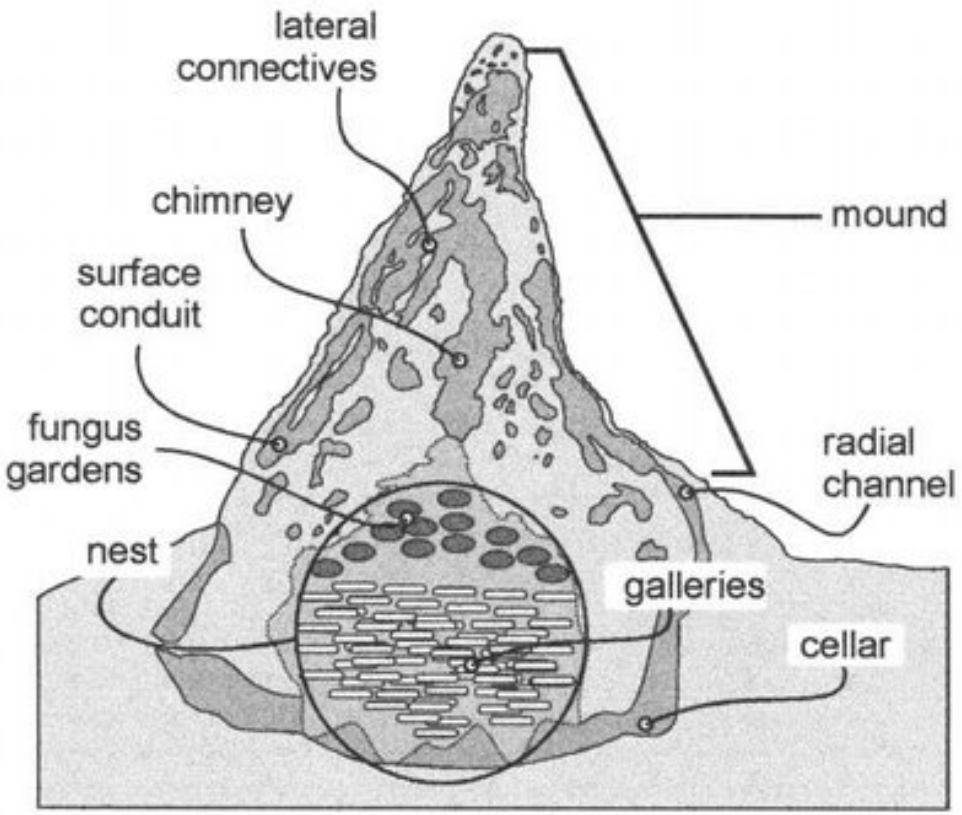
http://www.ozanimals.com/

Mate

Queen

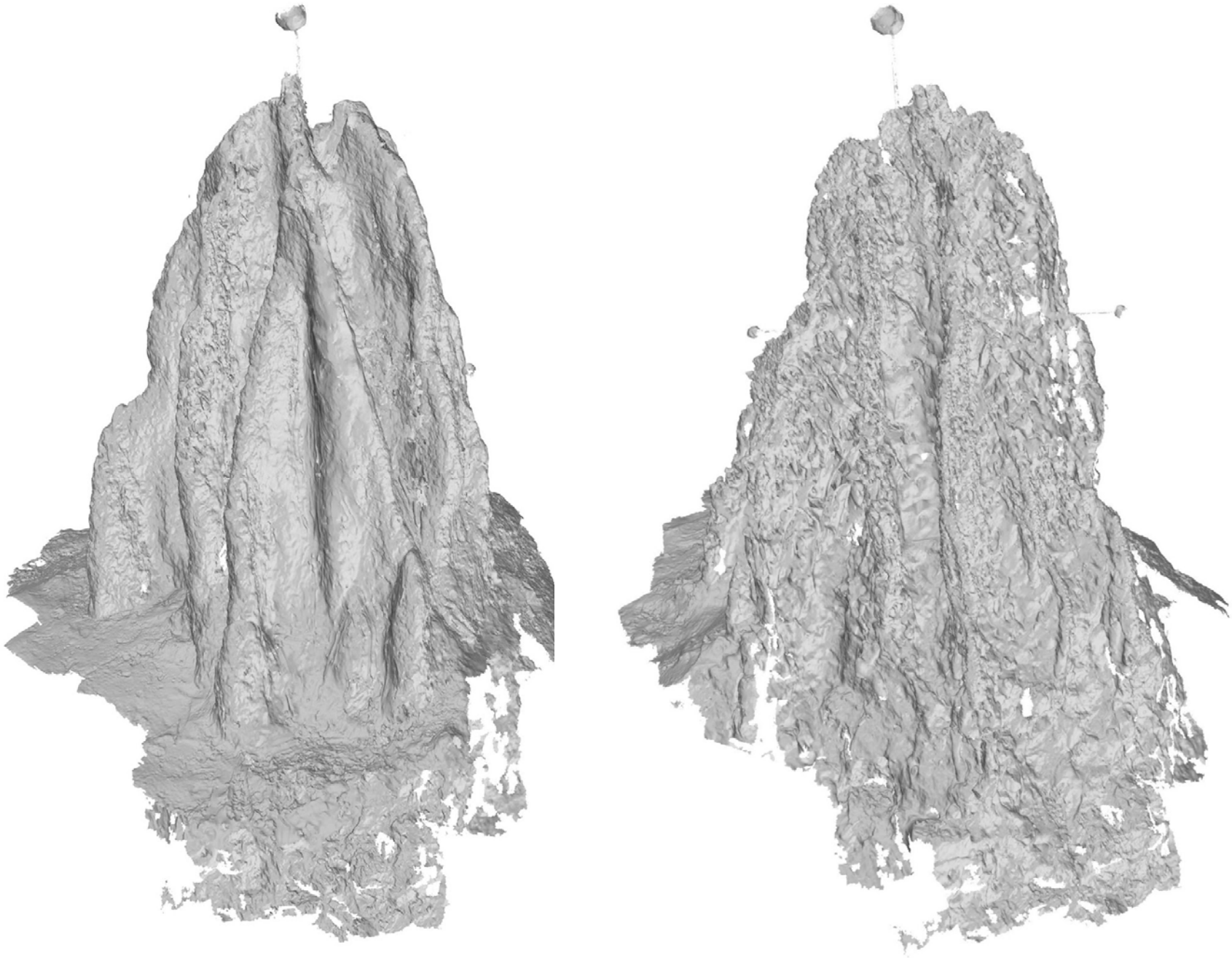
Soldiers and workers

# *Termite mounds have complex, dynamic internal geometry*



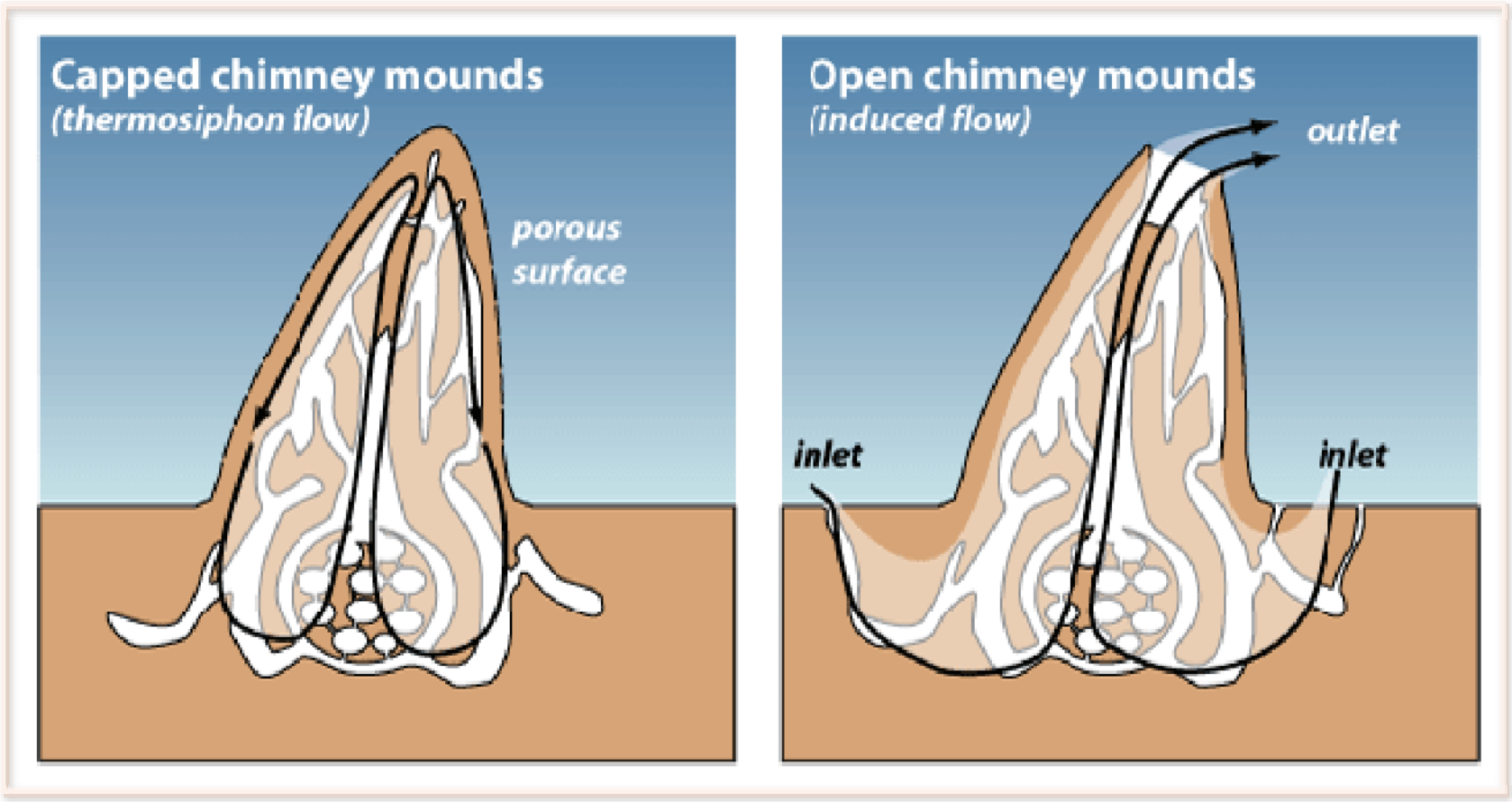

***Gypsum fill of a mound shows the intricate network of tunnels inside the mound***

**Courtesy: Rupert Soar, Pallavi Sharma**



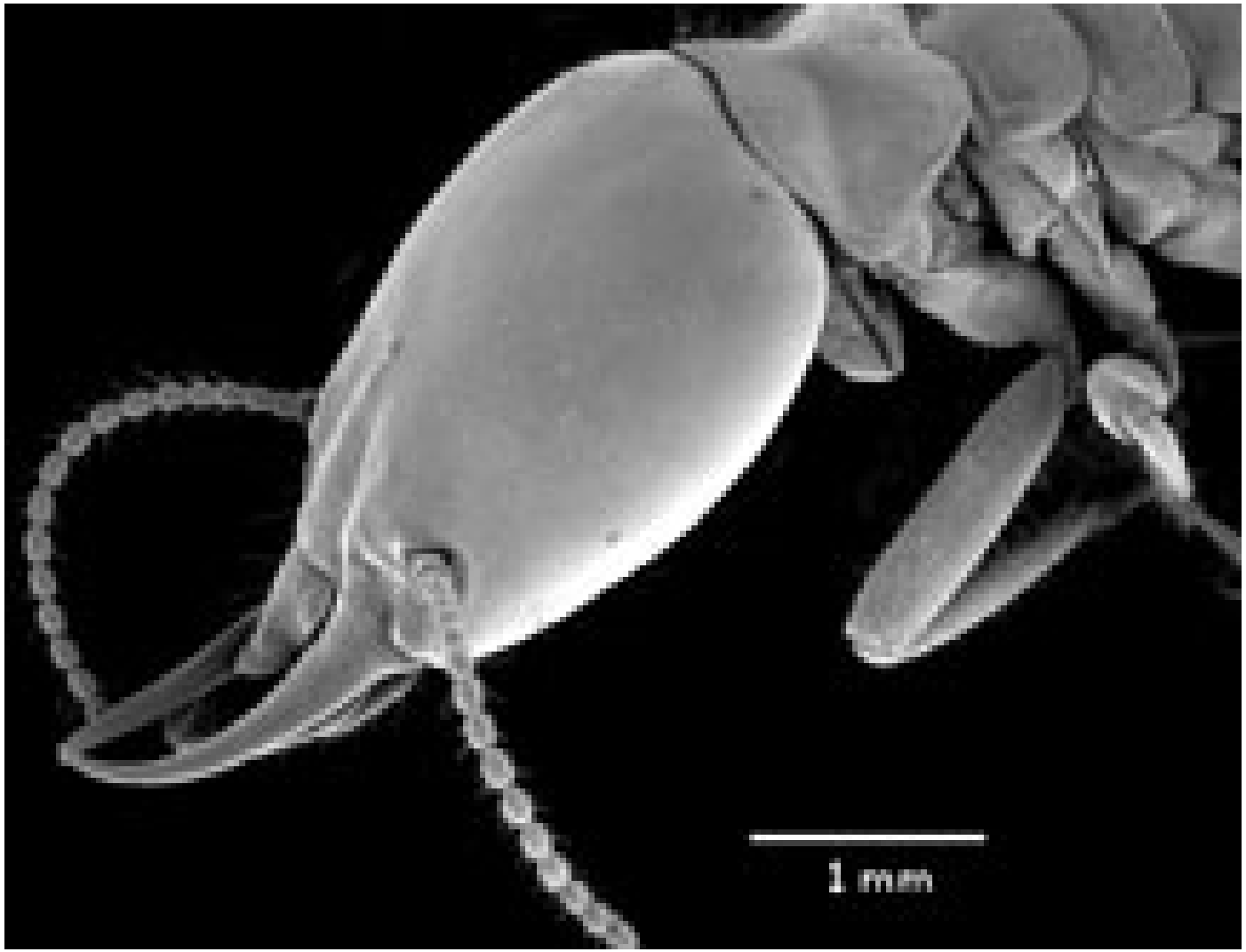
Courtesy: Rupert Soar, Pallavi Sharma

# *The extended phenotype hypothesis*
# *Termite mounds as gas exchange structures*




http://www.esf.edu/efb/turner/termitePages/termiteGasex.html

# Worker and soldier termites have no eyes (only alate termites have eyes)






http://www.africamuseum.be/museum/research/general/research-picture/termite

# *Termites as builders*

- **Major and minor workers continually modify and remodel the mound structure and maintain its structural integrity.**
- **They build by collectively depositing pellets of wet mud at the site of repair/ build by their mandibles**

# *Main questions*

- ***What is the function of the mound?***
- ***How do termites know where to build?***
- ***Do termites manipulate their building material?***
- ***What sensory cues guide individual termites in these building tasks?***

***Null hypothesis: Termite mound has no function.***

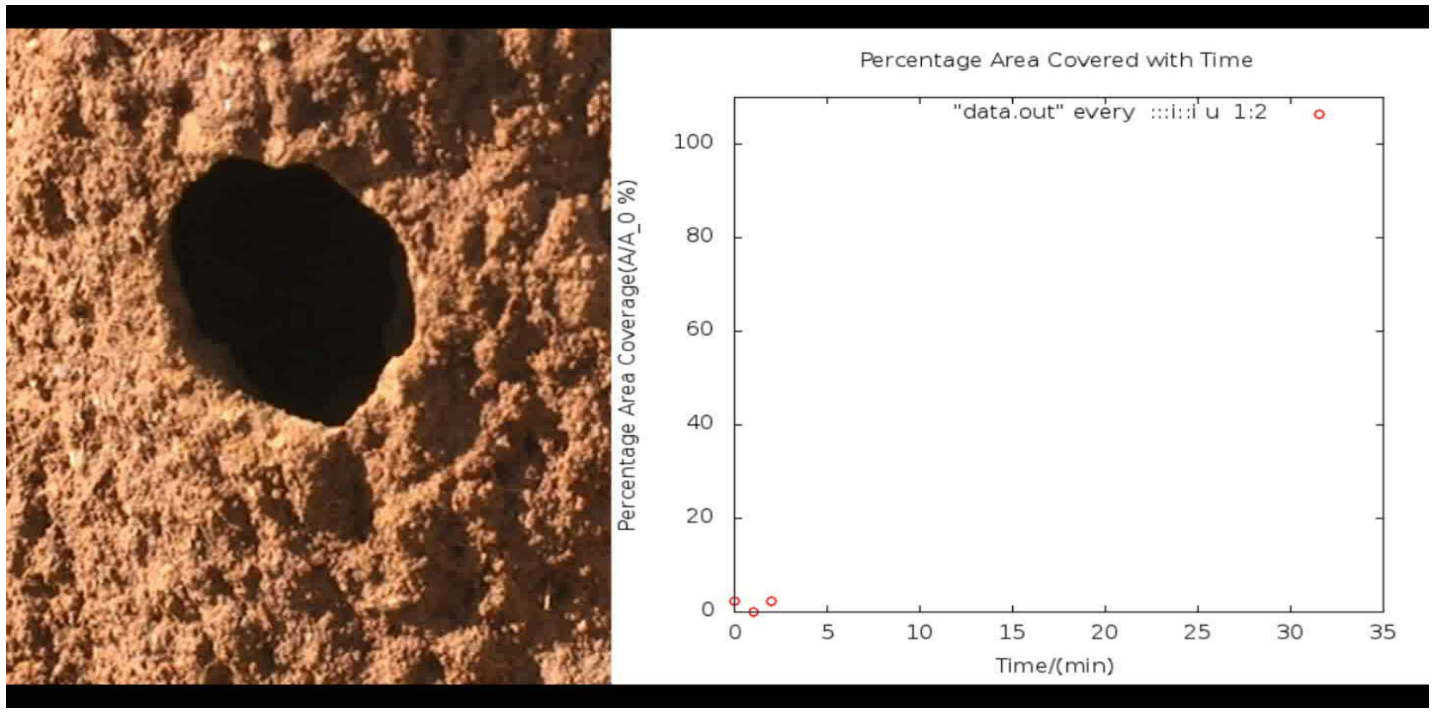
***Hypothesis:*** ***The mound serves no function. It is a side-product excavation and soil deposition.***

***Prediction:*** ***If true, termites should not respond to mound injury.***

# *Worker termites sense and immediately mend a breach in the mound surface*

**2 cm**

0 min | 10 min | 14 min | 18 min | 22 min | 23 min



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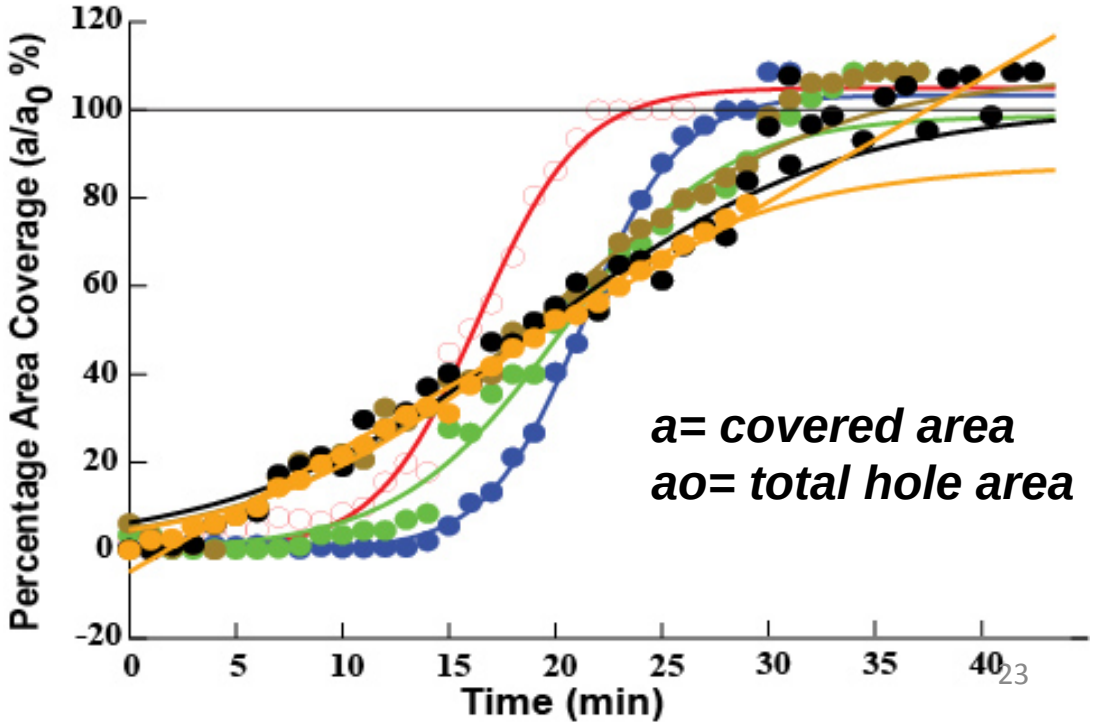


# *Worker termites sense and immediately mend a breach in the mound surface*

2 cm

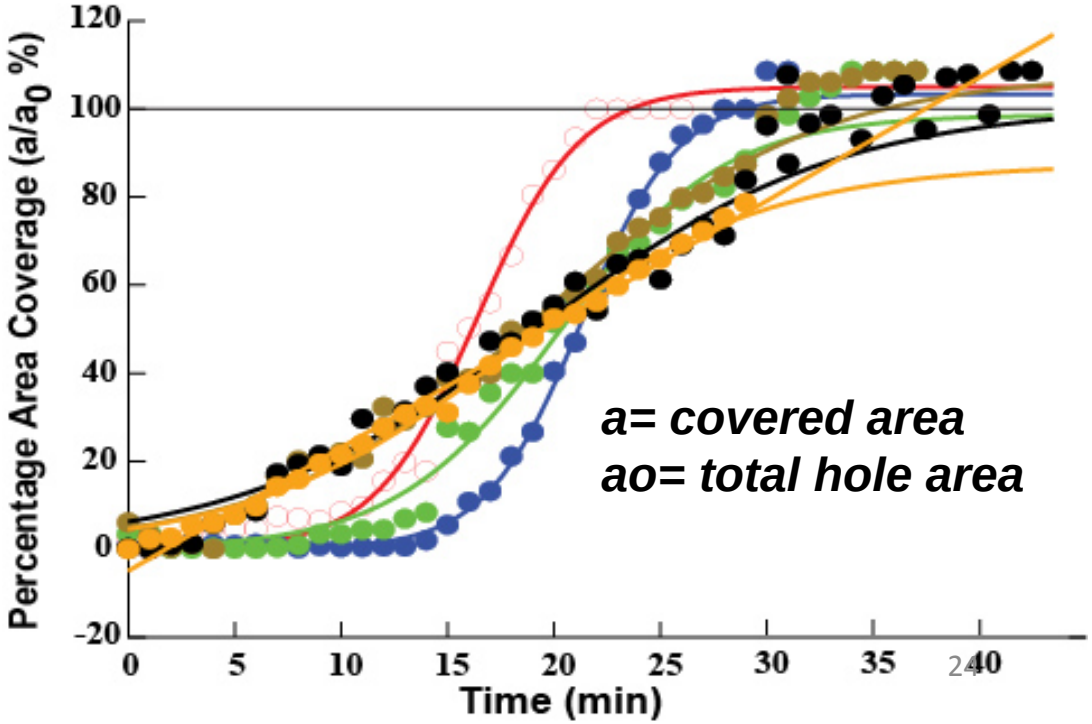
0 min | 10 min | 14 min | 18 min | 22 min | 23 min

**Sigmoidal curve suggests an exponential recruitment followed by de-recruitment of the termites.**

**Assumptions:**

**1. Rate of building is a good proxy for number of termites.**

**2. Each termites works at constant rate.**



# *Working hypotheses for mound repair*

***Sigmoidal function suggests a process of recruitment and de-recruitment.***

- ***Recruitment:***

  ***Chemically mediated:*** ***clay pheromone?***

  ***Mediated by sound:*** ***head vibrations etc?***

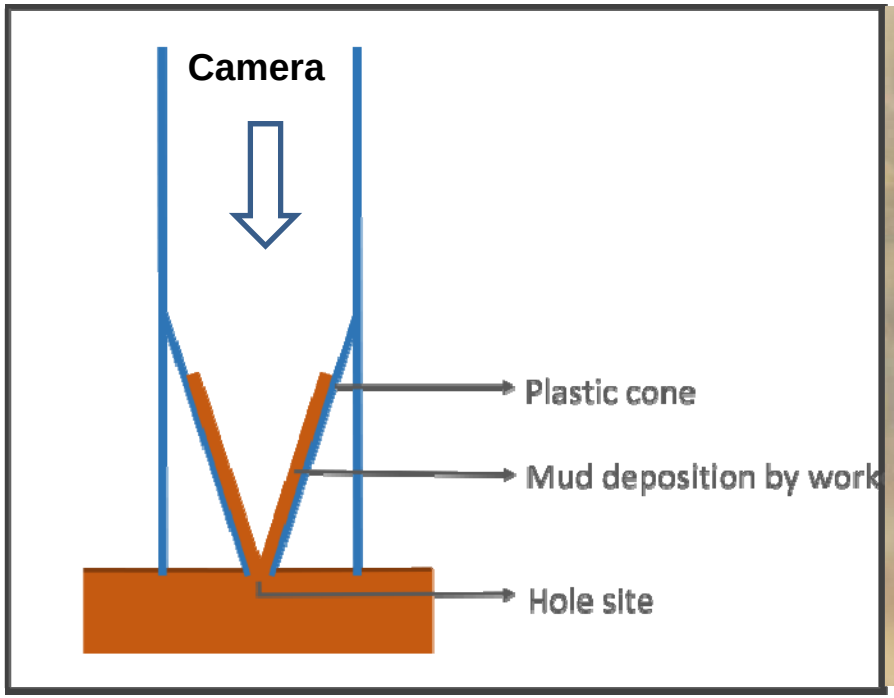
- ***De-recruitment:***

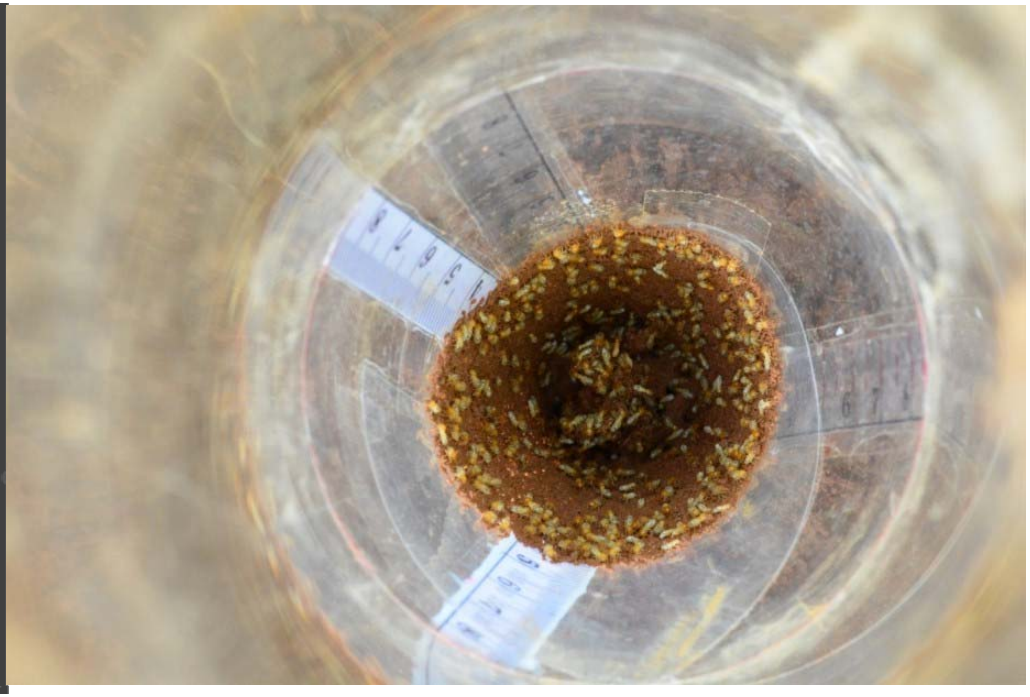
  ***Mechanically mediated:*** ***crowding / mechanosensory stimulation?***

***Other means?***

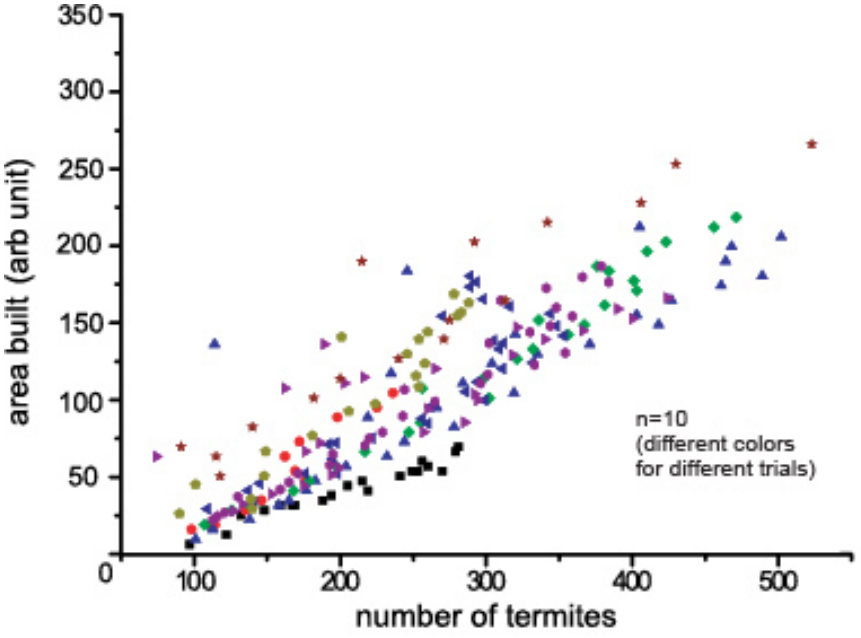
# *Is rate of building a good proxy for the number of termites?*

- *Open building in an inverted cone from a hole in the mound*
- *Termites build along the wall*
- *Camera on the top allows counting the number of termites*

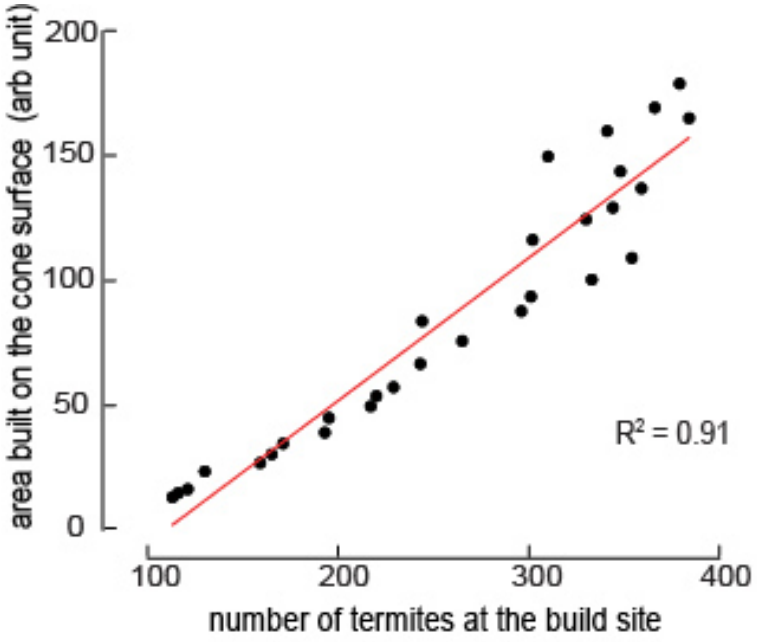


# *Area built is directly proportional to number of termites*




Scatter plot of area built in the cone against the number of termites at the building site. A fit to this data gives us a strong linear dependence ($R^2 > 0.9$)




Linear fit to data from one experiment. $R^2 = 0.91$

***Is rate of building a good proxy for the number of termites?***

***YES***

# *Building a mathematical model for hole repair dynamics*

1: The rate of area (a(t)) filling is directly proportional to the number of termites (n(t)) present at the site of repair.

2: The rate at which each termite lays a mud pellet is constant. **Thus, hole size (a(t)) can be used as proxy for number of termites (n(t)).**

$$\frac{da(t)}{dt} = \lambda n(t)$$

3: Recruitment and de-recruitment at the site of repair is number-dependent.

$$\frac{dn(t)}{dt} \propto n(t)$$

4: The recruitment happens by means of systemic sensory cues laid by each termite.

5: The effective rate of recruitment of termites also depends on the area of the hole available for the termites to work.

$$\frac{dn(t)}{dt} \propto [a_0 - a(t)]$$

$$\frac{d^2a}{dt^2} = ka_0 \frac{da}{dt}[1 - \frac{a}{a_0}]$$

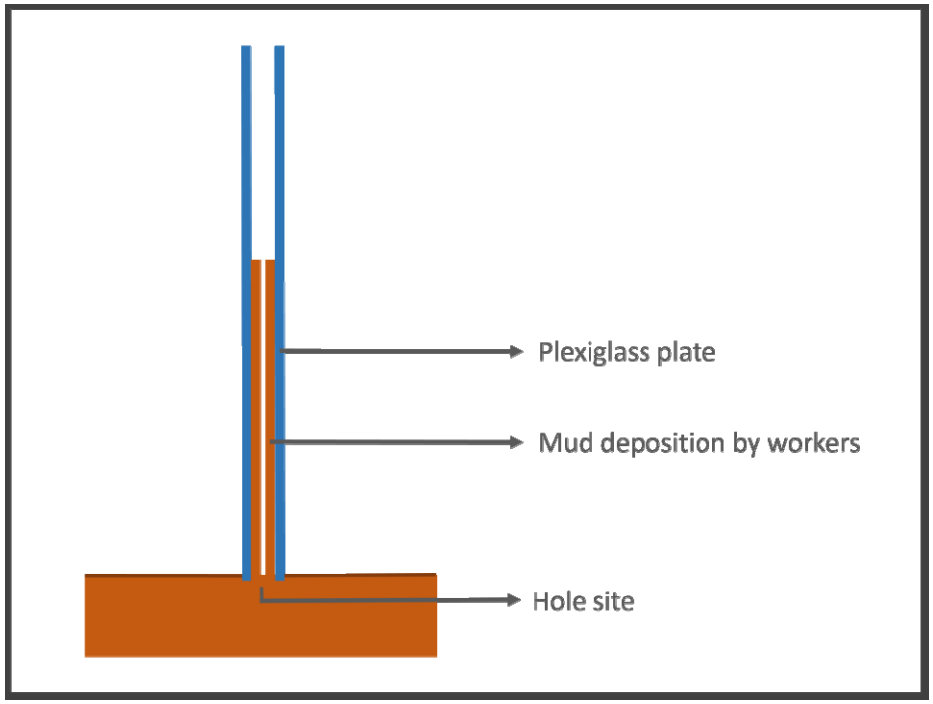
a(t): area filled by time t
a0: total area of the hole
c: experimentally determined constants

**Differential Equation**

$$a(t) = a_0[1 + c_1.\tanh\left(\frac{1}{2c_3(t + c_2)}\right)]$$

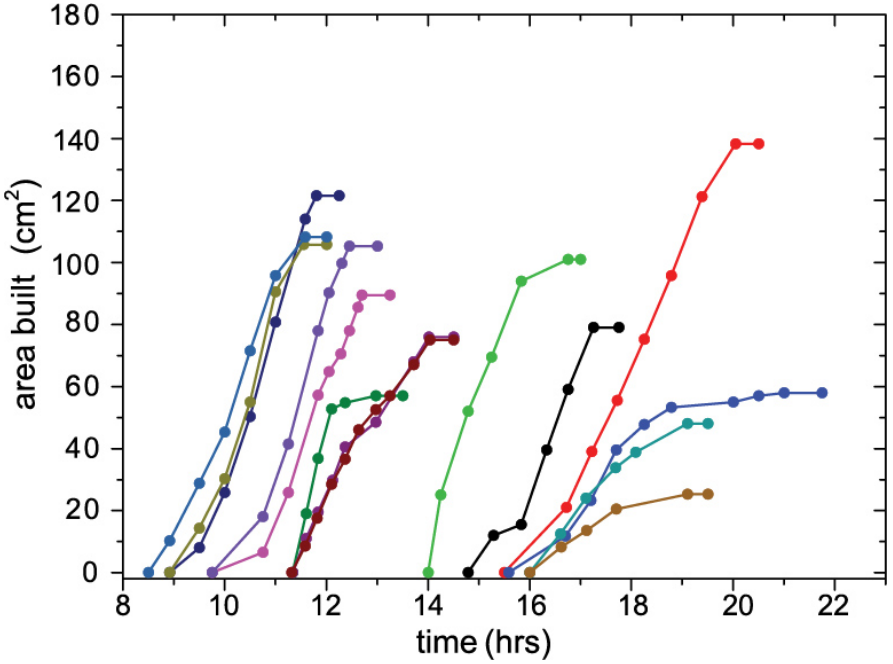
# *Hole repair activity varies through the day*

- *Confined extended arena around a hole in the mound elicits active mud transport in the arena*
- *Single pellet layer thick deposition on the plates*
- *Time-lapse images give the built area as a proxy for the amount of soil translocated*



# *Building rates vary depending on external environment*

**Snapshot from the experiment showing building happening in the parallel plate arena**

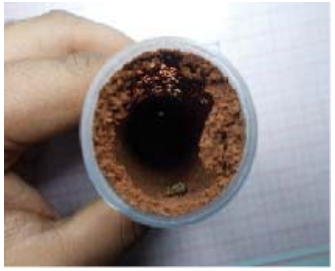


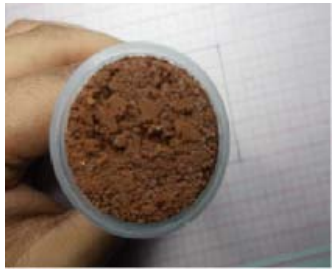

**Plots showing the growth in the arena with time.**
**Rates of building vary depending on the time of the day**

**Rates of building vary diurnally and seasonally**

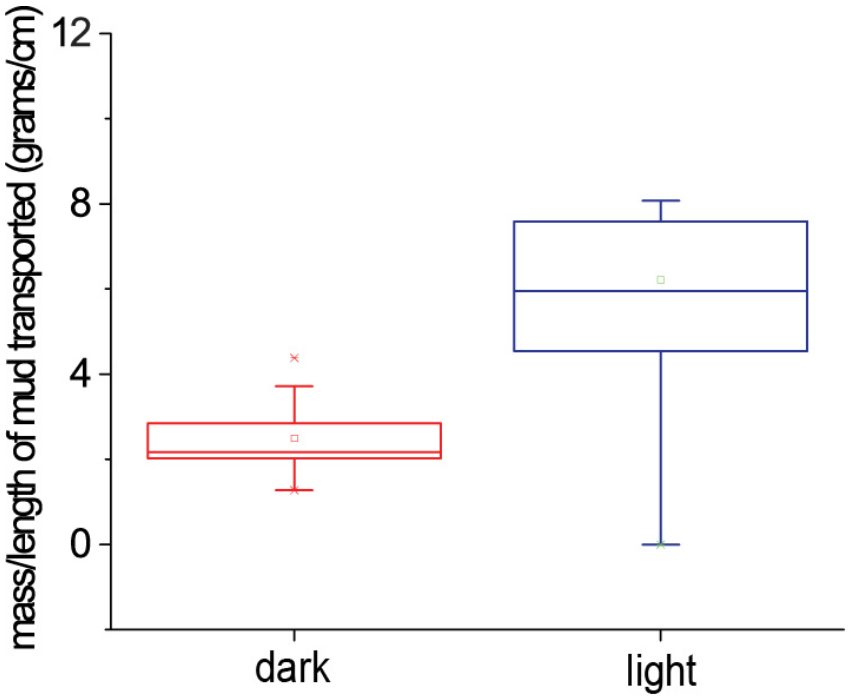
# Assay 1: Building in a tube

solid filling in the transparent tube and a hollow filling in the opaque tube after the experiment



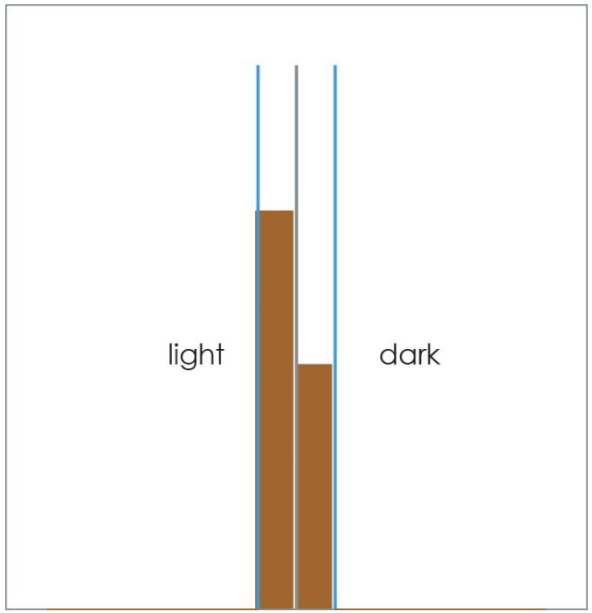


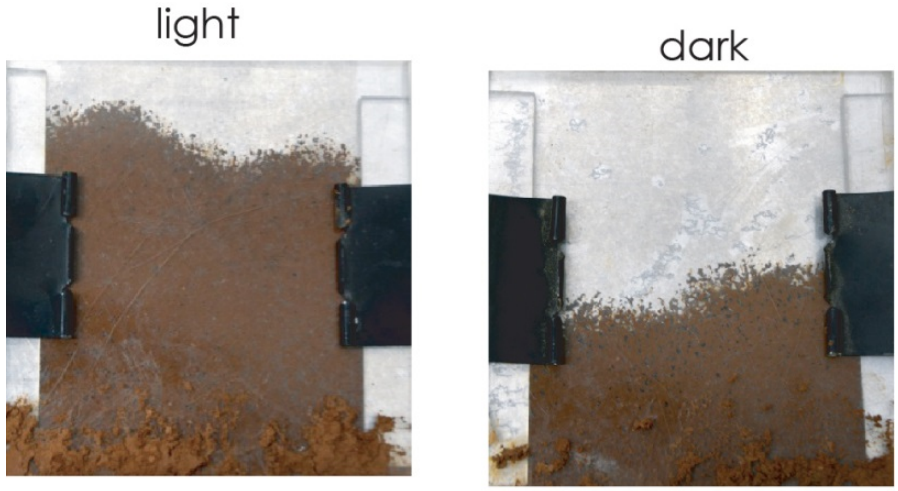
Two equal sized plastic tubes (one transparent to light and the other opaque) were inserted in two holes in a mound at the same height from the base and left undisturbed for 24 hours.




**Light intensity is a sensory cue!**

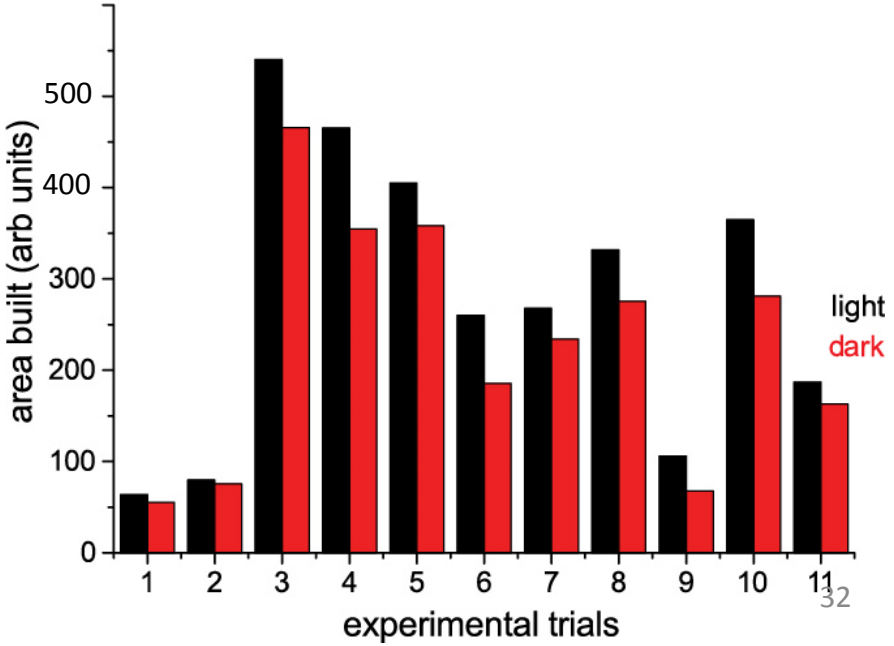
# *Assay 2: Two-dimensional plate*



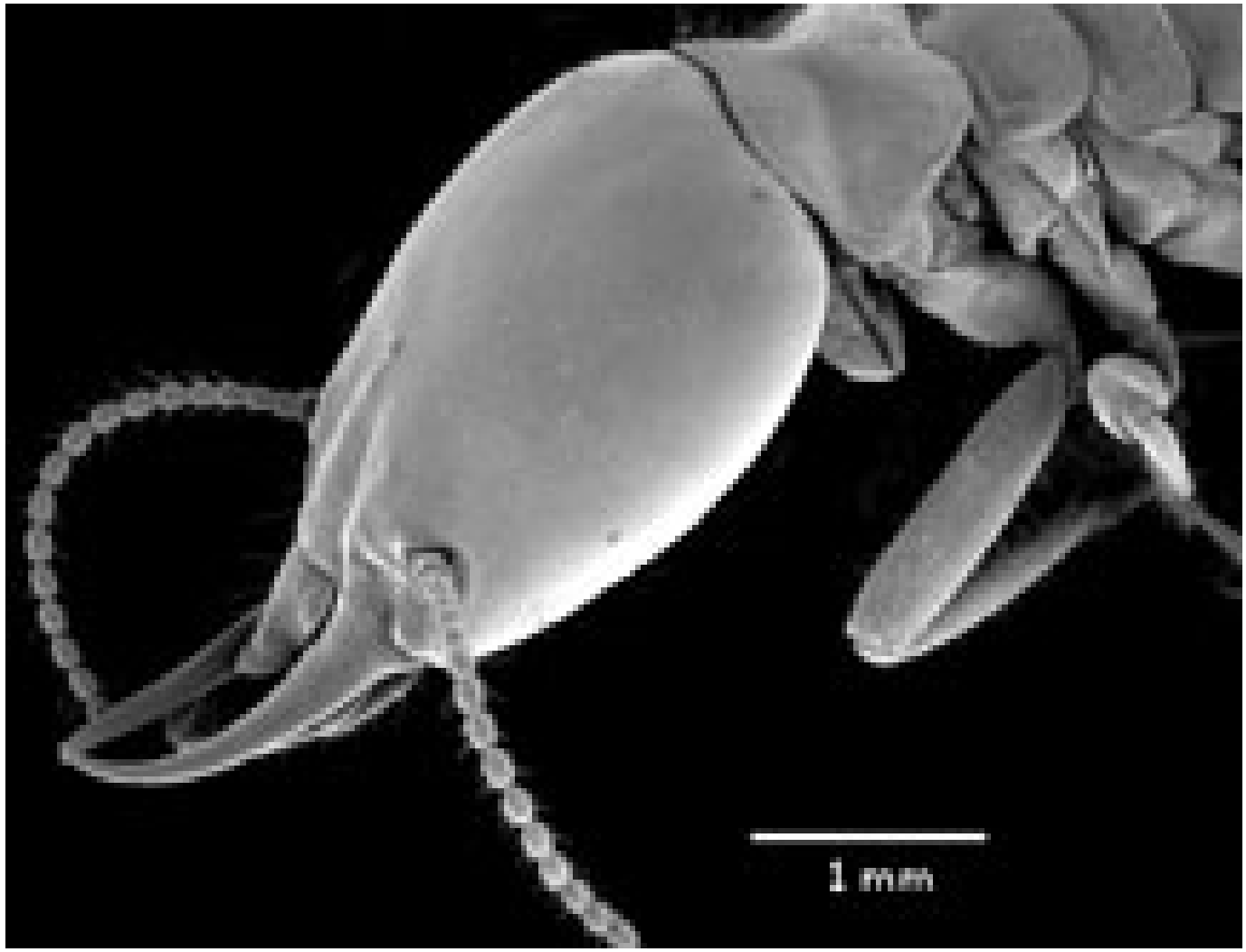

Amount of growth in light (>10000 lux) vs dark (<50 lux)

Double-spacer parallel-plate arena with an aluminium plate sandwiched between two plates, fixed atop a single hole in the mound.




**Difference in the rate of building under different luminosity conditions.**

# *Light acts as a sensory cue!*




http://www.africamuseum.be/museum/research/general/research-picture/termite

# *Termite Mounds as indicators of aquifers (from old Sanskrit texts)*

**जंबूवृक्षस्य प्राग्वल्मीको यदि भवेत्समीपस्थः ।**
**तस्माद्दक्षिणपार्श्वे सलिलं पुरुषद्वये साधु ॥ ३०४ ॥**

If there is an anthill near a jambu (Syzigium cumini) tree towards its east,
there will be good water at a distance of two purushas (~ av. length of a person's body) from there.
*(Surapala's Vrikshayurveda, verse 304, 10th century CE)*

**वल्मीकसंवृतो यदि तालो वा भवति नालिकेरी वा ।**
**पश्चात्षड्भिर्हस्तैर्नरैश्चतुर्भिः शिरा यस्य ॥११४॥**

If a taala (Borassus flabellifer) or naalikeri (coconut) tree is surrounded by anthills,
there will be an aquifer towards the west, at a distance of four purushas and six hastas
(one hasta = length of one hand (the length from the elbow to the tip of the middle finger).
*(Upavanavinoda, verse 114, 13th century CE, Author: Śārṅgadhara, son of Daḷmodara)*

# *Soil moisture also drives mound building*

Eruption of spontaneous fresh building after rains

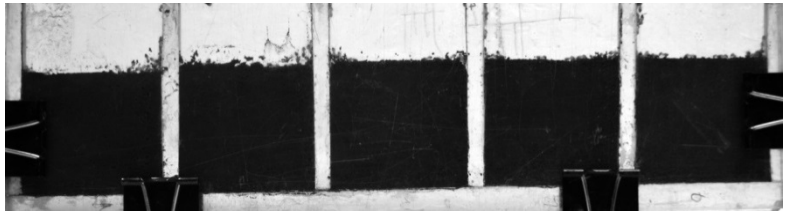
**Hypothesis: Soil moisture affects the rate and type of build.**

# *Soil moisture as a driving parameter for mound building*

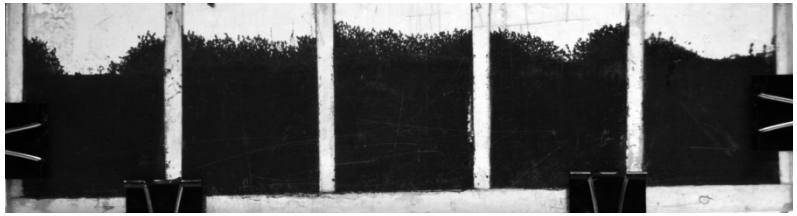
- 5 simultaneously running arenas
- Each with same weight of dry soil and 30 fresh major workers
- Varying amounts of water in each arena

Maximal growth at around 40% soil moisture

t= 0 min

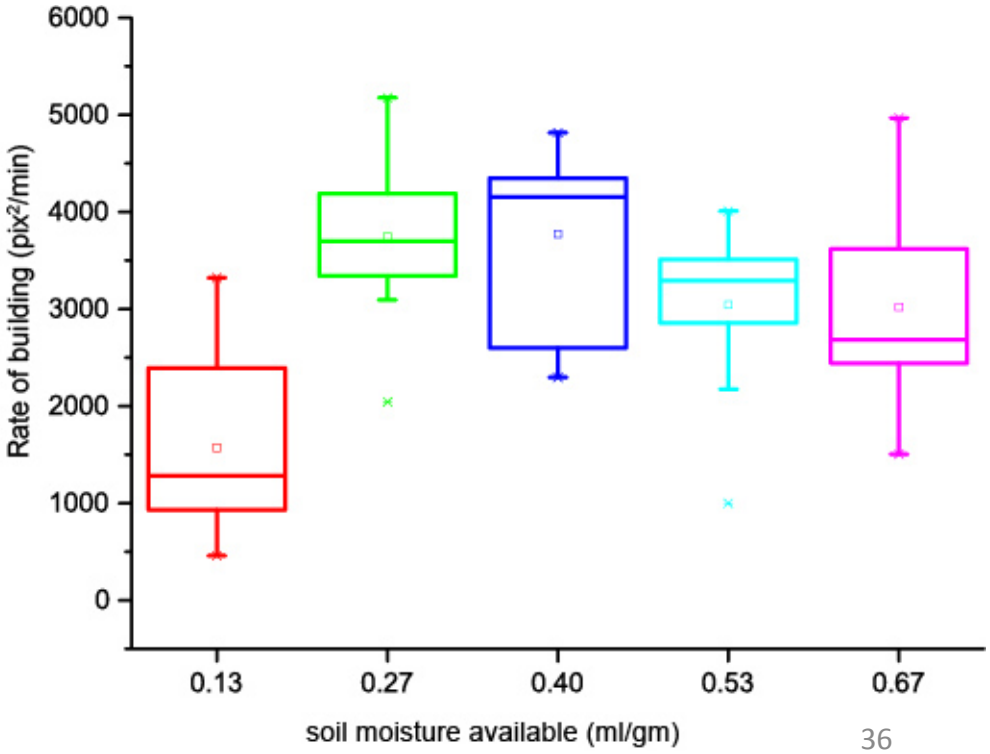


t= 45 min



0.13 0.27 0.40 0.53 0.67

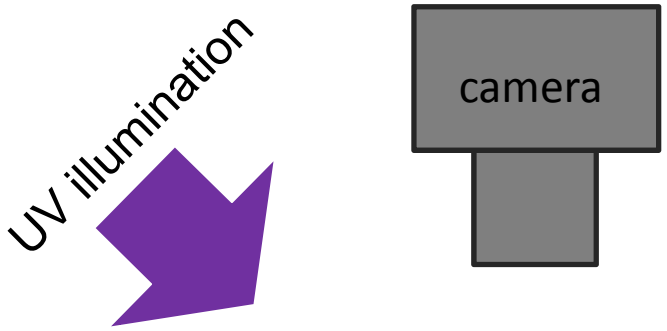
Soil moisture available



# *Do termites modulate soil moisture?*

- Moisture content of freshly built soil is constant ~ 18% despite different initial moisture conditions or environmental variations.
- Worker termites ingest soil in their mouth, regurgitate the soil and then egest a fresh pellet at the site of building.
- Observations of termites with swollen bellies within the mounds indicated that they may carry water.

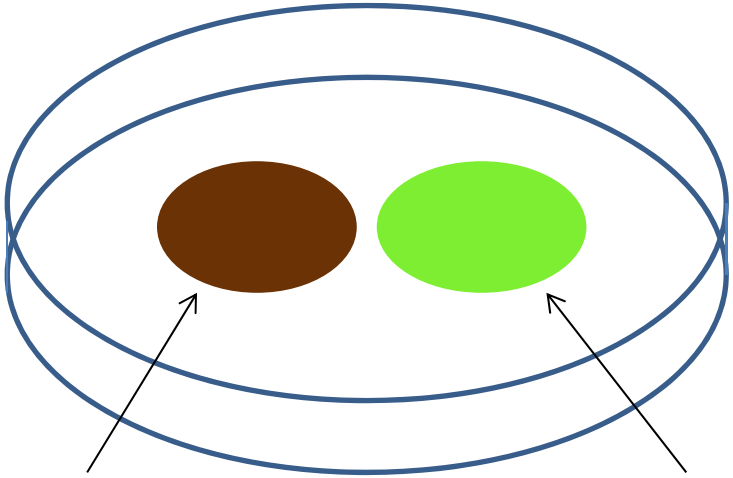
# *Fluorescein Assay*




**Termites were given two patches of soil to build.**

**One patch was moistened with water mixed with fluorescein**

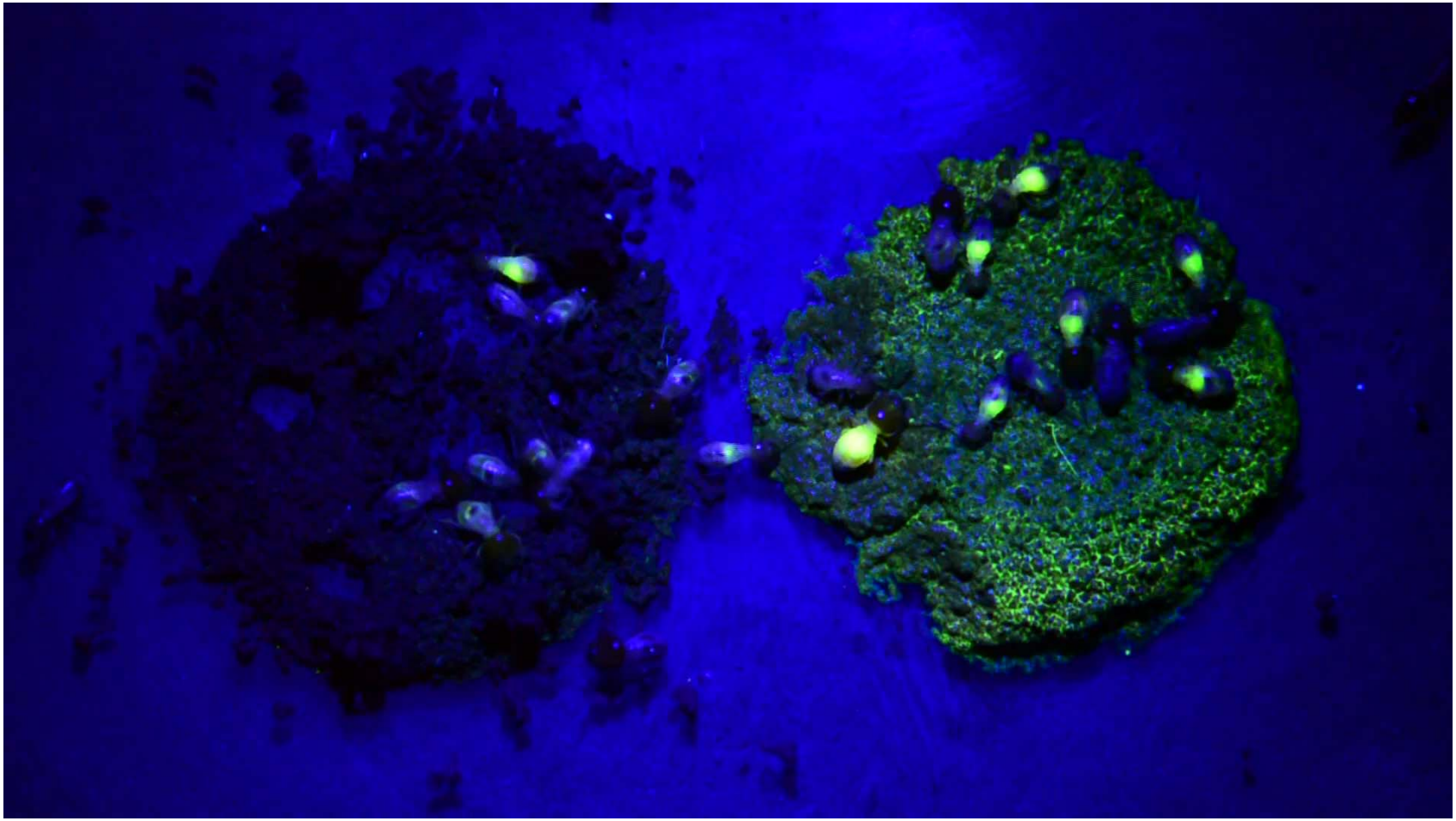
**The other patch was dry.**



dry soil patch

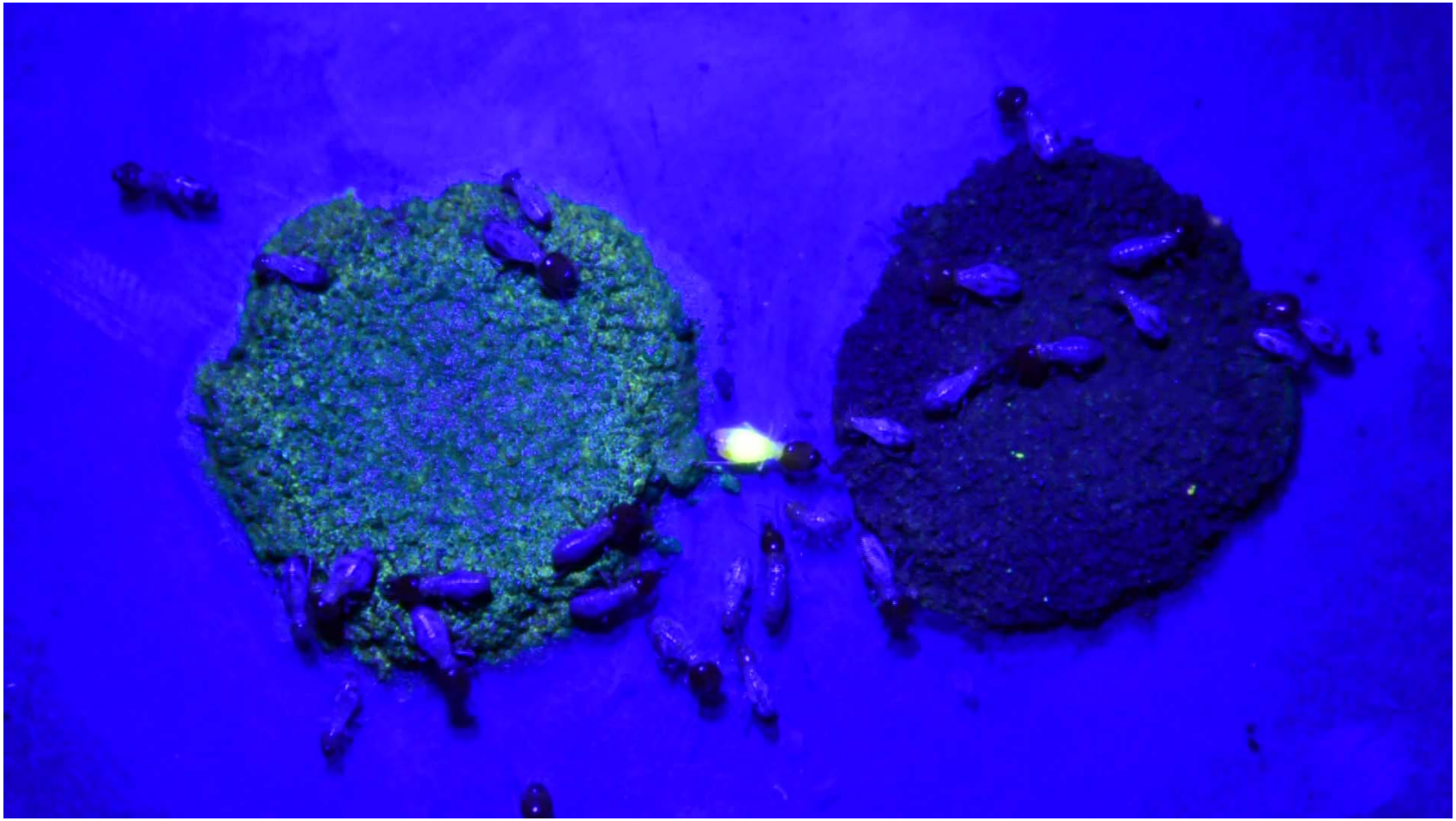
wet soil patch with fluorescein

# *Worker termites suction out water from wet soil*



Video sped up by 6X

# *Workers may exchange water*



Video sped up by 2X

# *Preliminary Observations*

- ***Worker termites actively transport water from wet patches of soil.***
- ***Water transport may be a cooperative exercise***
- ***Workers lose water from their body while building in dry soil***
- ***Termites modulate soil moisture levels***

# *Traffic rules in termites*

***Main Questions:***

***1. How do termites move in confined spaces?***

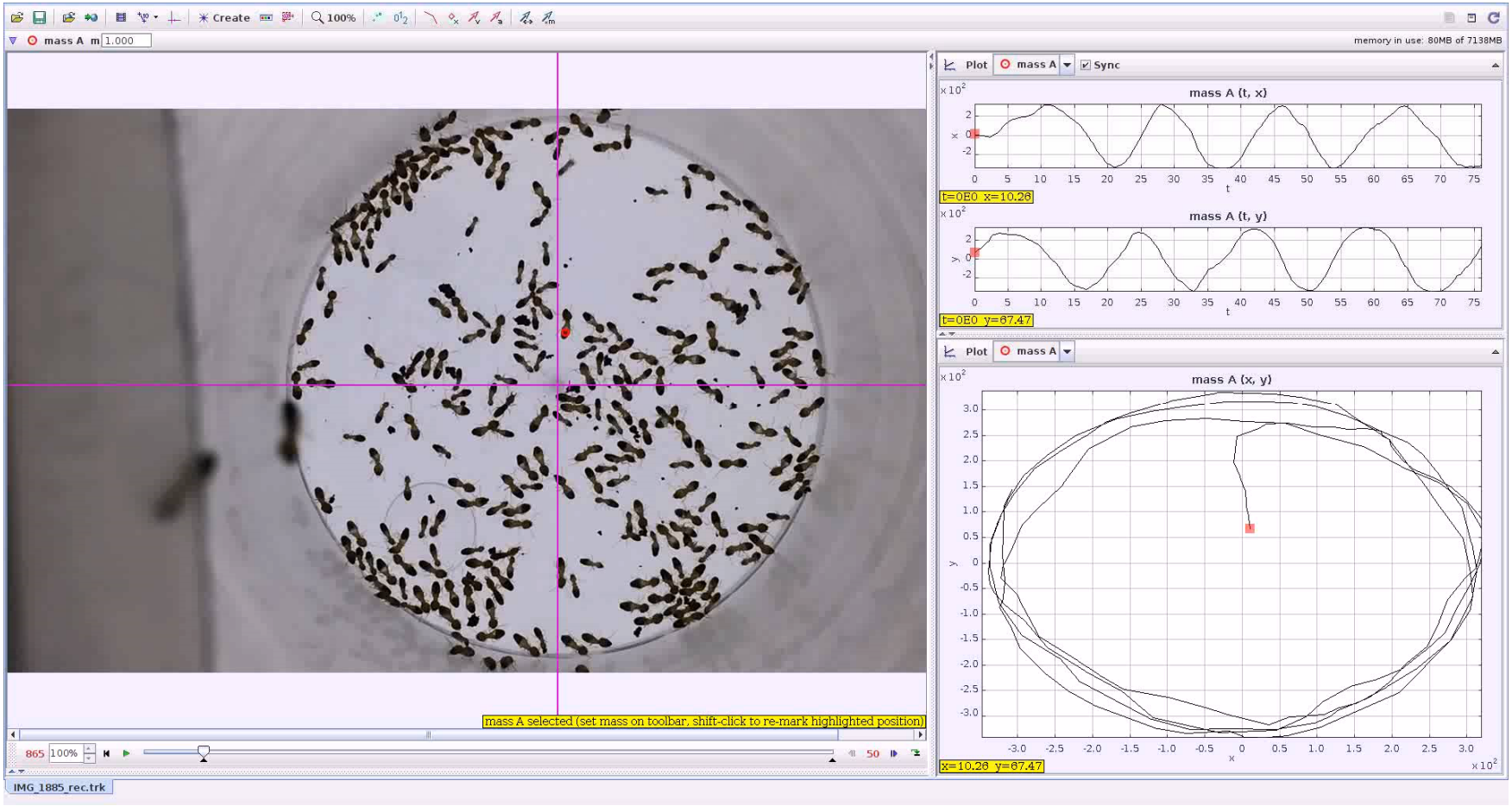
***2. How do termites avoid a traffic jam?***

***3. What cues guide termites to follow traffic rules?***

# *The Milling Assay*

**Termites in a confined space transition from their disordered state to highly ordered milling behaviour,**

# Quantification of milling behaviour



# *The milling assay*

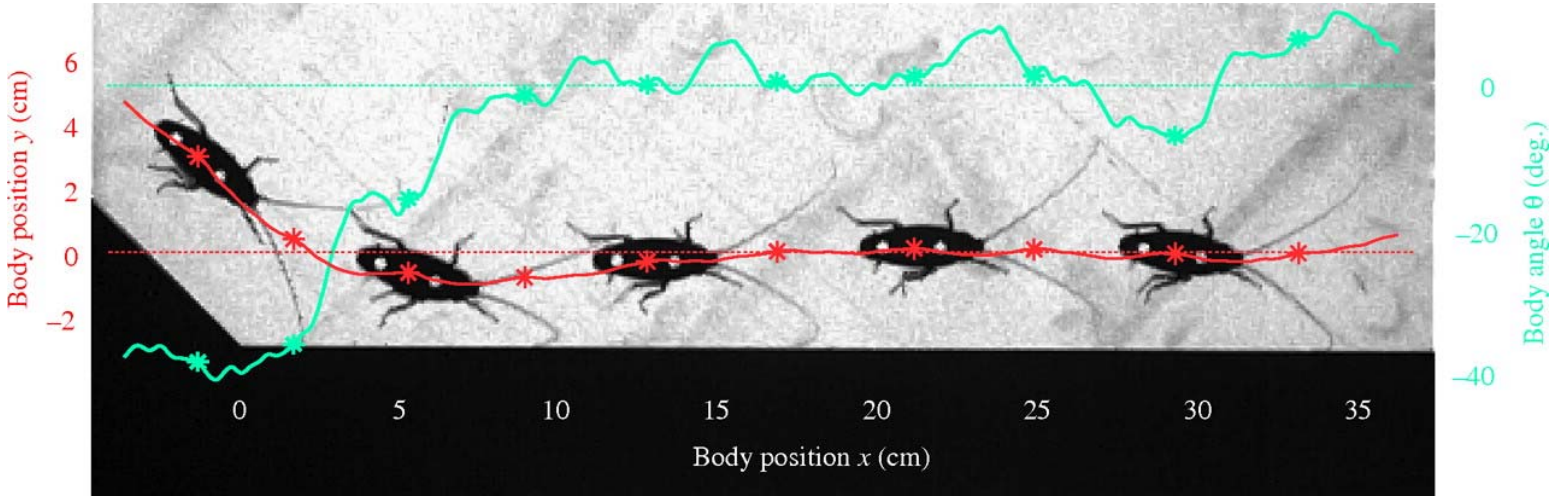
**Hypothesis 1: The milling behaviour is not density-dependent, but a summative outcome of individual-level responses.**

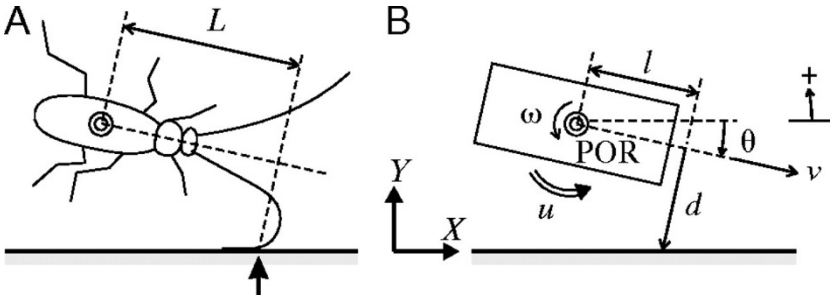
Termites, like cockroaches, show wall-following behaviour. Multitudes of individual wall-followers hence look like milling termites.

**Hypothesis 2: The milling behaviour is density dependent, and occurs as a result of collective activity.**

Requires a critical mass to work.

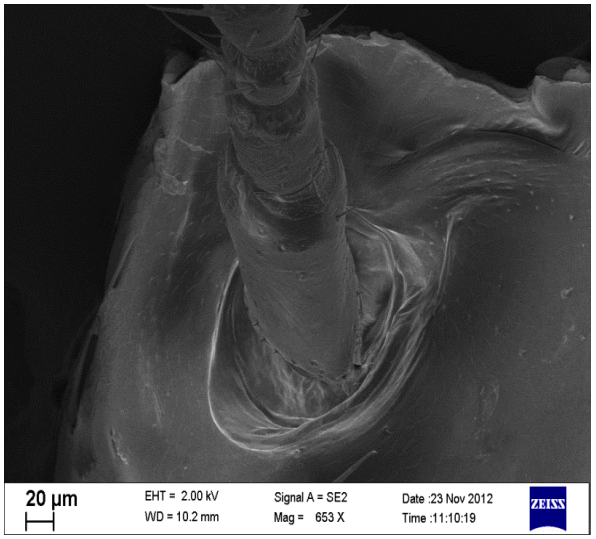
# *Wall-following behaviour in cockroaches*



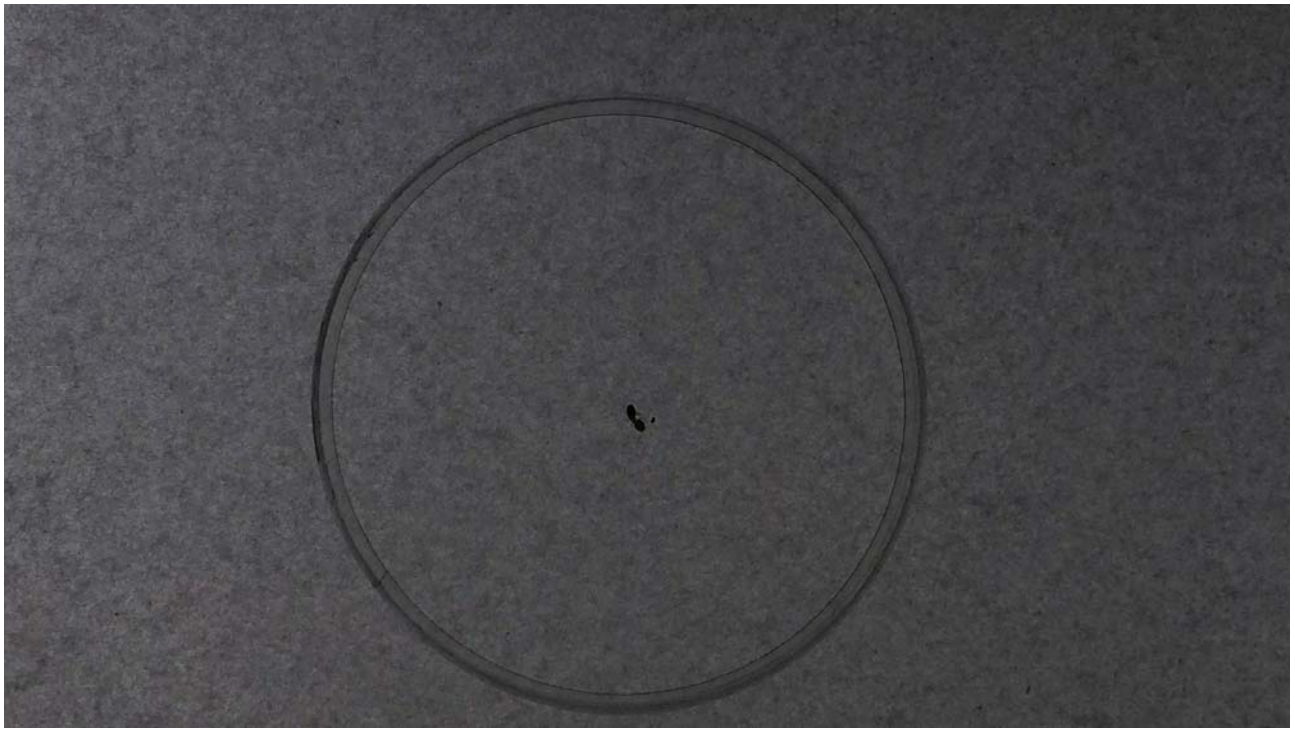




**N. J. Cowan et al. J Exp Biol 2006;209:1617-1629**

# *Do single termites mill?*




**Termite antennal mechanosensors can mediate the onset of milling**



# *Is milling behaviour the outcome of many individual level responses?*

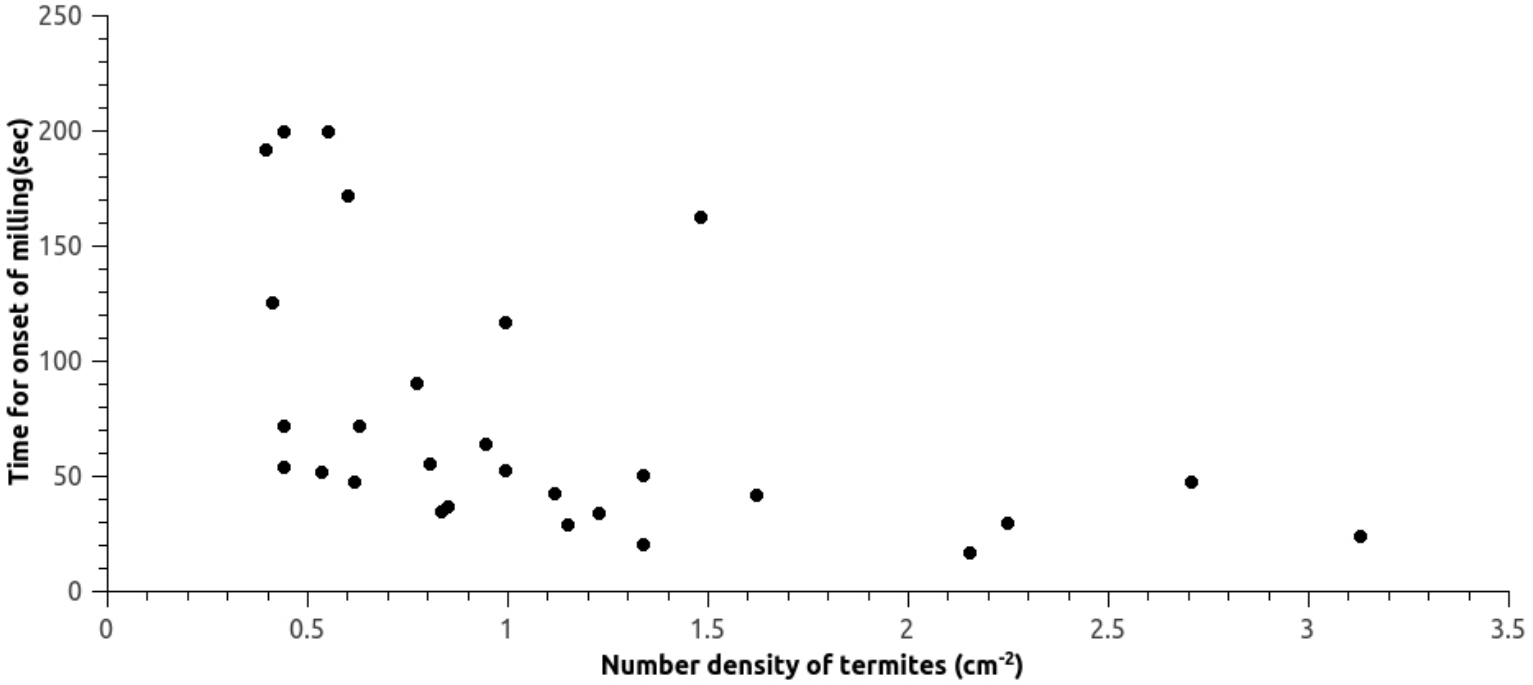
- ***The onset of milling behaviour is probably mediated by antennal mechanosensors.***

- ***Because individuals can travel in either direction, in a circular arena, this can cause a traffic jam and bring traffic to a standstill.***

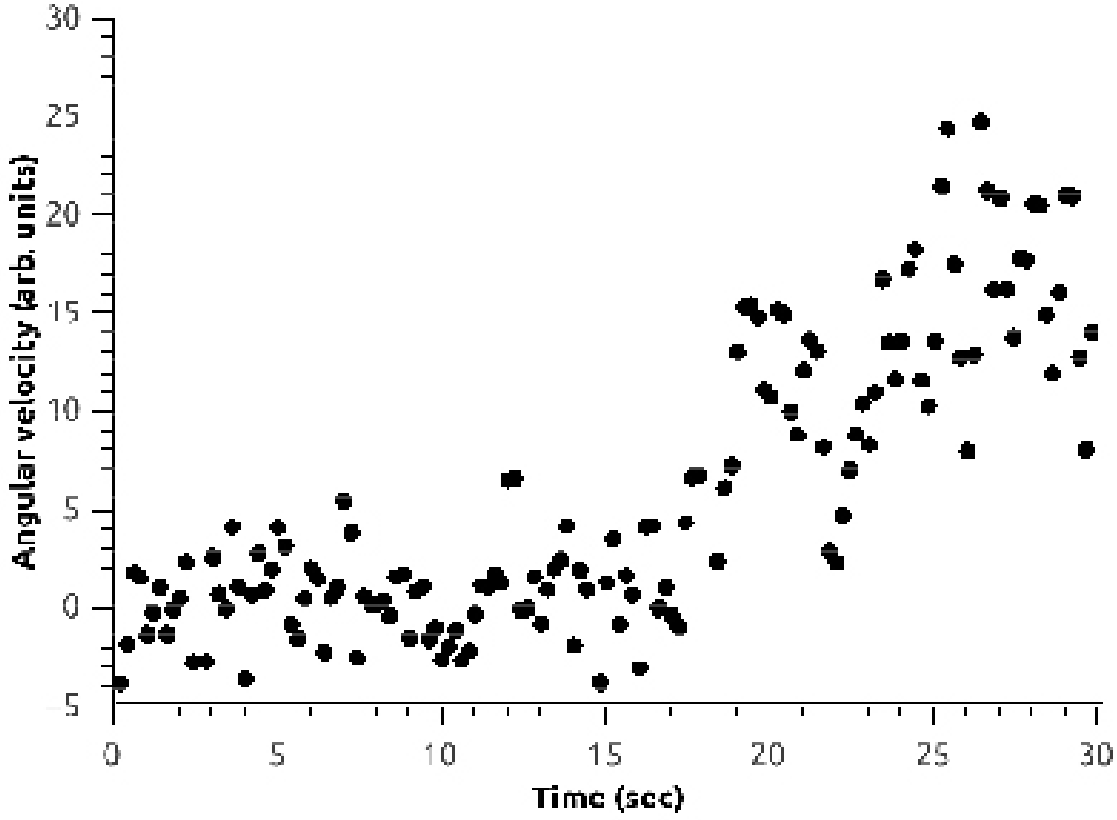
- ***How do termites avoid traffic jam?***

# *Collective milling is density dependent (video)*

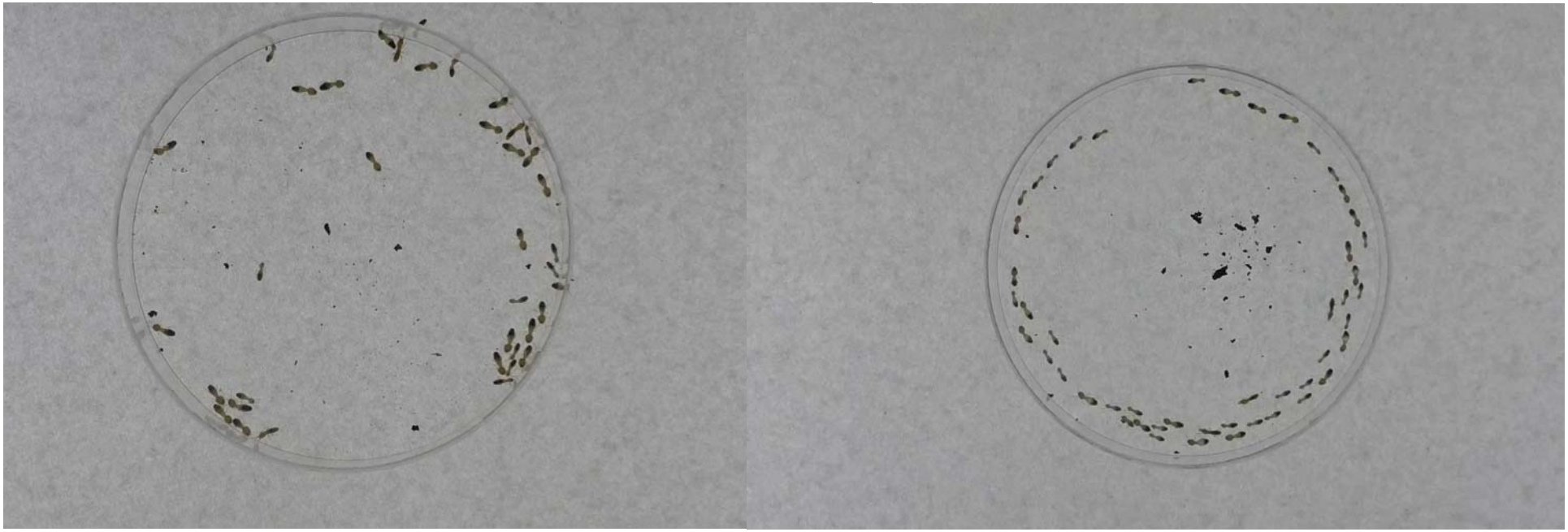
# *Collective milling is density dependent (plot)*



# …and speeds their transport



# *Do termites use only mechanosensory cues for milling?*



***Hypothesis:*** ***Chemical trails guide termite movement***

# *Disruption of chemical trails causes disruption of termite milling*

# *Chemical trails drive movements across species*

***Odontotermes redemanni lays trail***

***Odontotermes obsesus follows trail***

## Chemical trails in termites: sternal glands

# *Conclusions*

- ***Termites use a combination of mechanosensory feedback and chemical pheromones to move in their confined environs.***
- ***These cues establish a trail which termites follow.***
- ***Milling behaviour is density-dependent. More the merrier.***
- ***It greatly reduces time of transport***
- ***Chemical cues are not species-specific.***

# *Conclusions and future questions*

***Integrity of mound structure is actively maintained by termites: What is the mound function?***

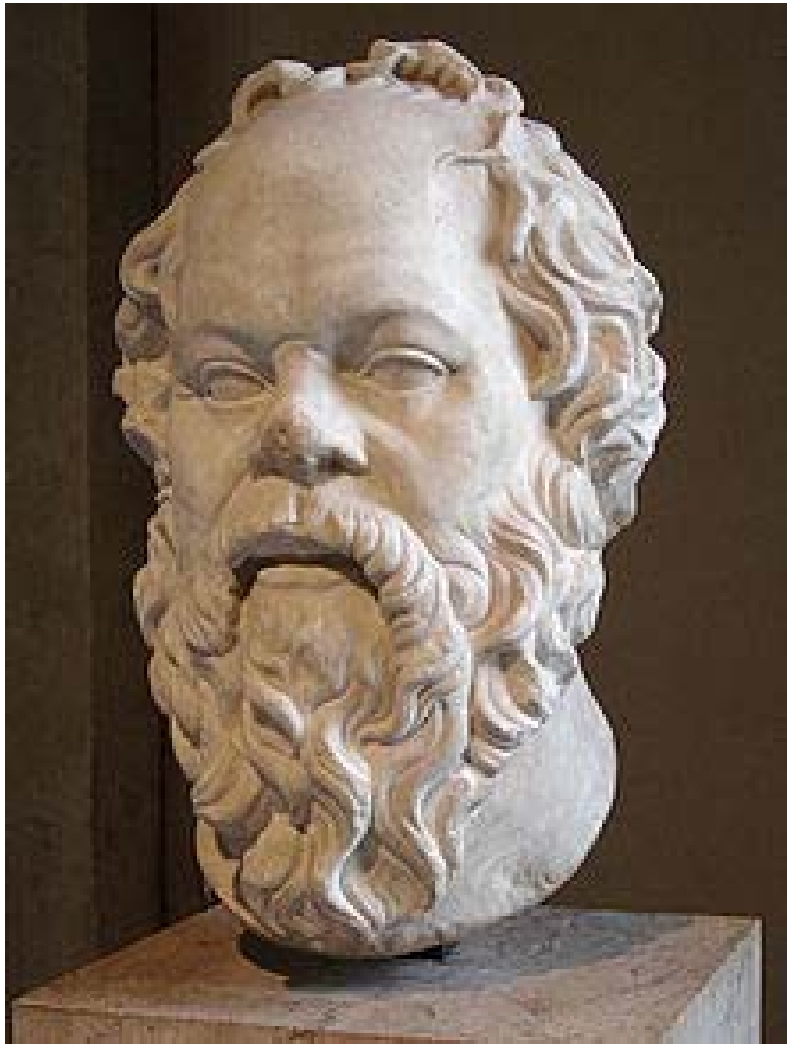
***They sense light via some non-ocular means to detect a breach in their mound: Where is this sense located?***

***There is active recruitment and de-recruitment of termite numbers: How are these mediated?***

***Soil moisture is important for mound structure and building activity: How do termites modulate soil moisture?***

**….stay tuned!**

# *Socratic Wisdom….and the wonderful boundlessness of our ignorance*



***Socrates (469-399 BC)***

# *Acknowledgements*

**Sreekrishna Varma Raja P.C.**

**Amritansh Vats**

**Chandan Pandey**

**Parmeshwar Prasad**

**Shivam Chitnis**

**Lakshmi Ramesh**

**Iqbal “Boots” Bhalla**

**Paul Bardunias**

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