Termites as models of swarm cognition

J. Scott Turner

Abstract Eusociality has evolved independently at least twice among the insects: among the Hymenoptera (ants and bees), and earlier among the Isoptera (termites). Studies of swarm intelligence, and by inference, swarm cognition, have focused largely on the bees and ants, while the termites have been relatively neglected. Yet, termites are among the world's premier animal architects, and this betokens a sophisticated swarm intelligence capability. In this article, I review new findings on the workings of the mound of *Macrotermes* which clarify how these remarkable structures work, and how they come to be built. Swarm cognition in these termites is in the form of "extended" cognition, whereby the swarm's cognitive abilities arise both from interaction amongst the individual agents within a swarm, and from the interaction of the swarm with the environment, mediated by the mound's dynamic architecture. The latter provides large scale "cognitive maps" which enable termite swarms to assess the functional state of their structure and to guide repair efforts where necessary. The crucial role of the built environment in termite swarm cognition also points to certain "swarm cognitive disorders", where swarms can be pushed into anomalous activities by manipulating crucial structural and functional attributes of the termite system of "extended cognition."

Keywords Swarm Cognition · Termites · Macrotermes · Stigmergy · Superorganism · Social insect

1 Introduction

One of the most remarkable examples of convergence among the animals is the independent evolution of eusociality in two distantly related groups of insects: the Hymenoptera (the ants,

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bees and wasps) and the Isoptera (the termites). Despite their disparate histories, these two orders of social insects have evolved virtually identical social structures: populous colonies consisting of assemblages of sterile workers, often differentiated into castes (including a caste of fertile individuals that can serve as reproductive propagules for the colony) that are the offspring of one or at most a few reproductively competent individuals (Wilson 1971). This type of social structure has often been likened to a "superorganism", in which the colony has many of the attributes of a more conventionally defined organism, including physiological and structural differentiation, coordinated and goal-directed action, and so forth (Wheeler 1911; Novikoff 1945; Moritz and Southwick 1992; Golley 1993).

Among the organism's cardinal virtues is cognition, whereby the organism comes to be informed of its environmental context (Kandel et al. 1991; Bechara 2002). If the superorganism concept has validity, one would expect that it, too, should be imbued with this virtue, that is, social insect colonies should be capable of cognition at the superorganismal scale (Millonas 1994; Hutchins 2000; Bechara 2002). Indeed, it has been argued that cognition itself is fundamentally a social phenomenon, whether the units of the social system are neurons in brains or organisms in societies. That the social insect superorganism indeed has cognitive powers has been well demonstrated through the ability of insect swarms to respond adaptively to environmental context, or to solve large-scale problems that are beyond the ken of individuals within the swarm to solve on their own (Bonabeau et al. 1999).

The study of swarm phenomena has been overwhelmingly the province of only one of the two eusocial insect orders, the Hymenoptera, and among those, it is the ants that have garnered the most attention (Table 1). In contrast, the "other" social insects, the Isoptera, or termites, account for only a small proportion of the interest. In part, this reflects the disparate diversity of the different orders: there are only about 2,400 species of termite world-wide (Krishna and Weesner 1969), compared to more than 20,000 species of bee alone (Michener 2000) and roughly 12,600 species of ants (Agosti and Johnson 2005). Robustness in laboratory culture, the tendency of certain species to emerge as "model" organisms as more becomes known about them, and other factors may also account for the disparity in attention. Whatever the source of the bias, the striking convergence in social structure betokens a (largely unstudied) convergence of social cognition.

If cognition is, by its nature, a social phenomenon, it is also, by its nature, an environmental phenomenon. Thus, swarm cognition, if it is to be studied, let alone recognized, must account for the environmental context in which it evolved: where the swarm lives, the nature of its habitat, the problems it must solve and the information it needs to solve them. This means that the study of swarm cognition must be grounded on a solid foundation of natural history. Although termites have long been recognized as presumptively cognitive superorganisms, on a par of sophistication with their hymenopteran cousins, just how sophisticated

Table 1 Results of a Google Scholar® search for distribution of swarm intelligence studies among the eusocial insects

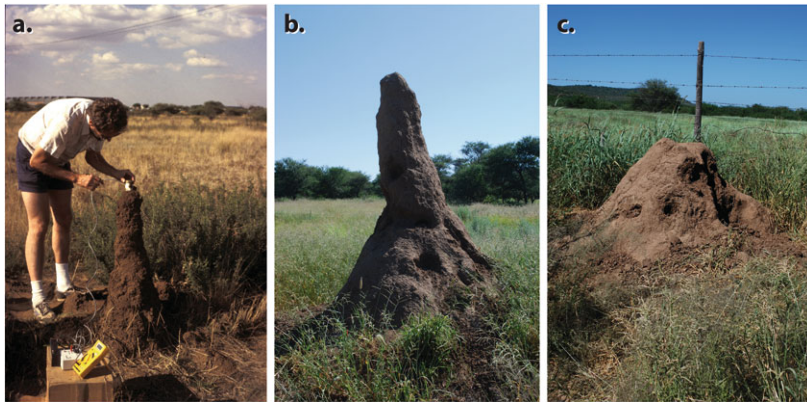| Search terms			Hits All fields	Hits Biology only
Swarm intelligence	AND	Ant	7, 500	1, 020
		Bee	960	638
		Wasp	354	412
		Total Hymenoptera	*8,814*	*2,070*
		Termite	425	209

Fig. 1 Three examples of macrotermitine mounds. (**a**) An open chimney mound of the genus *Odontotermes*. (**b**) A closed chimney mound built by *Macrotermes michaelseni*. (**c**) A closed-chimney mound built by *Macrotermes natalensis*

their cognitive abilities are has been obscured somewhat by a poor understanding of the natural context for those cognitive abilities.

Among the world's most sophisticated animal architects are the mound-building termites of the genus *Macrotermes* (Harris 1956; Weir 1973; Mitchell 1977; Collins 1979; Darlington 1986; Dangerfield et al. 1998; Turner 2001; Turner and Soar 2008). These termites build immense structures of remarkable complexity and coherency, which serve essentially as wind-driven lungs for the colony (Fig. 1). This sophisticated architecture betokens a sophisticated swarm cognitive ability: termites must not only "know" how to build such a structure, but also whether the structure they have built is the "correct" one.

In this article, I will outline some of our recent work on these "other" social insects, their collective behavior and the structures they build, in the hope the veil can be lifted a little on what appears to be a remarkably sophisticated system of swarm cognition. I will set the context by outlining the elements of the mound and colony system (Sect. 2), and the mechanisms of mound construction (Sect. 3) and maintenance (Sect. 4). What emerges from these findings is an unexpected role for water as a major organizer of termite swarm behavior (Sect. 5). From there, I outline new findings on the cognitive world of termite swarms (Sect. 6). These have led to the identification of several "swarm cognitive disorders" (Sect. 7) which provide insight into how swarm cognition works in these insects. I conclude with a broader discussion of whether cognition can even exist in the context of insect swarms and the structures they build (Sect. 8).

2 The problem

Termites of the genus *Macrotermes* live in colonies consisting of 1–2 million individuals, contained in a compact subterranean nest (Darlington 1990). *Macrotermes*, as the name implies, are among the largest of the termites, with worker masses of about 14–15 mg, so that a single colony can contain several kilograms of termites. *Macrotermes* have also adopted the remarkable habit of fungiculture, maintaining in the nest a culture of a symbiotic fungus, *Termitomyces* spp., which aids in the digestion of the woody cellulose from the grass and wood that constitute the colony's main forage (Batra and Batra 1967, 1979; Wood and

Thomas 1989; van der Westhuizen and Eicker 1990; Darlington 1994; Rouland-Lefevre 2000; Aanen et al. 2002). The biomass of the fungal culture far exceeds that of the termites themselves, as does its metabolism. The collective metabolic rate of the colony, termites and fungus, adds up to an impressive rate, probably on the order of about 100 watts (Darlington et al. 1997), roughly the equivalent of a mammal the size of a goat. Just as it must be in a goat, this high metabolic rate must be supported by a commensurably high rate of exchange of respiratory gases. This is where the mound comes in.

Mound structure varies between species of *Macrotermes*, but their structures fall within two broad categories, which we term open-chimney and closed-chimney mounds (Fig. 1). In both designations, the chimney refers to the largest tunnel in an extensive reticulum of large-caliber vertically-biased tunnels that permeate the mound. In open-chimney mounds, this central tunnel opens at the top of the mound (Fig. 1(a)). In closed-chimney mounds, the top is capped (Figs. 1(b), (c)). Our focus has been on two species that build closed-chimney mounds, *Macrotermes michaelseni* and *M natalensis*. Of the two, *M michaelseni* builds taller mounds, with a conical base topped by a prominent spire that rises 2–3 meters tall. *M natalensis* mounds are shorter, typically 1–2 meters in height and usually consisting of the conical base only.

In both species, the mound is a device for capturing wind energy to power respiratory gas exchange for the colony (Turner 1994, 2001, 2002, 2005). Its function is quite complex, and the structure of the mound and nest are important mediators of this function (Fig. 2). The nest, where the termites actually live, consists of a spheroidal space that is typically about 1.5 m in diameter, and contains within it 50 to 100 oblate open spaces called galleries. Each gallery contains a "fungus comb", which is a complex folded structure constructed by nest workers from macerated wood slurry brought back to the nest by foraging workers (Fig. 3). During its construction, the comb is inoculated with fungal spores which germinate and digest the woody forage into more easily digestible oligosaccharides, which constitute the termites' actual diet (Rohrmann 1978; Wood and Thomas 1989; Darlington 1994). Each gallery is connected to its neighbors by one or two small portals roughly 3 mm in diameter, large enough for termites to move through (Fig. 3). The base of the chimney penetrates into the center of the colony and is constructed from excavated remnants of abandoned galleries (Fig. 2). Consequently, the air mass of the mound connects to the nest through several of the small portals that commonly connect galleries to one another. Peripherally, the nest is surrounded by a subterranean reticulum of large tunnels that open above into the mound reticulum, and peripherally to the extensive network of foraging tunnels that radiate several tens of meters from the nest. The subterranean reticulum also connects to the nest periphery through the same type of small portals that connect the galleries to one another. The mound air spaces, meanwhile, connect to the outside air through an extensive series of so-called egress tunnels that are rooted in the superficial tunnels of the reticulum, the so-called surface conduits (Fig. 4). Egress tunnels tend to occur in egress complexes, tortuous reticula of small-caliber tunnels that originate from a single entry point on the surface conduit and extend to just below the surface, separated from the outside air by a very thin layer of sand grains. The mound surface is underlain by hundreds of these egress complexes, and these make the mound surface porous.

For some time, it was thought the mound supported the colony's respiratory gas exchange by active ventilation of the nest, either through boundary layer effects of wind on the mound, or metabolism-driven natural convection within the mound and nest (Lüscher 1961; Darlington 1985). For *M michaelseni* at least, we now know this to be incorrect (Turner and Soar 2008). Nest ventilation requires that the nest air and mound air are well-mixed. In fact,

Fig. 2 Structural elements of the mound and nest of *Macrotermes michaelseni*. Plaster casts depicted here and in Fig. 4 were made in collaboration with Dr Rupert Soar. (**a**) Exposed plaster cast of the above ground tunnel network of a *Macrotermes michaelseni* mound. (**b**) A slice cut through a plaster filled spire at mid height. Note large tunnels in the center grading to smaller tunnels peripherally. (**c**) A vertical section through the nest viewed laterally. Note the chimney outlined by *dashed line* penetrating into the nest center, and the small openings that connect the chimney to surrounding galleries. (**d**) Exposed plaster cast of the subterranean reticulum. Ground level is indicated by the *dashed line*. (**e**) Exposed plaster cast of the center of the mound reticulum. (**f**) Partially exposed plaster cast of a surface conduit festooned with egress complexes. **ch**: chimney; **co**: colony; **ec**: egress complex; **ga**: gallery; **re**: reticulum; **sc**: surface conduit; **sre**: subterranean reticulum

nest air and mound air constitute two distinct air masses that mix poorly with one another. Mixing is impeded both by the nest structure (i.e., by the narrow and limited connections between galleries, between nest and chimney, and between nest and subterranean reticulum). Mixing is further impeded by stable thermal stratification between nest and mound, owing to nest temperature being frequently cooler than mound temperature. Gas exchange therefore does not occur by direct ventilation of the nest, but through a complicated interaction with turbulent wind that promotes mixing across the stable boundary between nest air and mound air.

Fig. 3 Fungus comb galleries and portals. (**a**) Fungus combs in situ in their galleries. (**b**) A section of gallery wall showing one of the portals that allow access and air flow between adjacent galleries. **fc**: fungus comb; **ga**: gallery; **gw**: gallery wall; **po**: portal
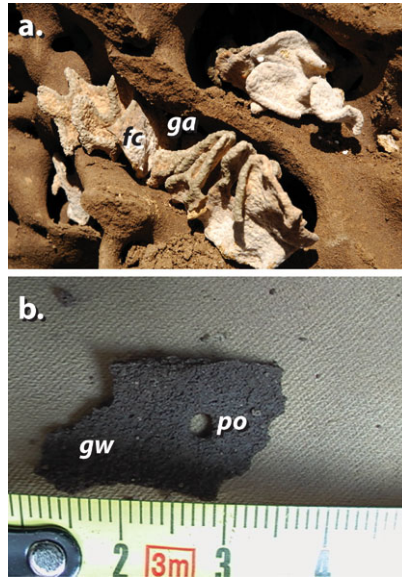
The mound does this by acting as a sophisticated filtering device for turbulent winds (Fig. 5). Natural winds are almost always turbulent, which means their energy is partitioned into two broad components: a "DC" component, consisting of steady wind, overlain by an "AC" component, consisting of transient fluctuations of velocity. Bulk flow of air through any structure is essentially DC work, and is limited by the structure's hydraulic resistance to flow. Wind can also do AC work, but in this instance the work is limited by the AC analogue to resistance, namely impedance. Unlike hydraulic resistance, which has no time dimension, impedance depends upon the frequency of the AC energy. One can use Fourier analysis to parse these transient fluctuations into a spectrum of discrete sinusoidal frequencies. Doing this for turbulent winds commonly reveals them to be broad spectrum, with wind energy distributed across a wide range of frequencies.

This is germane because the mound and nest together comprise a sophisticated impedance device which acts as a low-pass filter of the broad spectrum of turbulent wind energy (Fig. 5). Near the mound surface, the filtering is minimal, and flows there are driven strongly by a broad range of turbulent frequencies (Turner 2001). As one goes deeper into the mound, the high frequencies are filtered out, leaving only the lower AC frequencies to drive flow there. Within the nest itself, these transient fluctuations are virtually *nil*. The overall effect of this complicated filtering is that nest air is whipsawed between relatively high-frequency transients at the periphery (conveyed to the nest via the subterranean reticulum), but low frequency components in the center (where the nest air and mound air connect via the base of the chimney). This produces a slow-motion "sloshing" of the boundary between nest air and mound air, promoting occasional mixing between the two. In the chimney, these appear as periodic "puffs" of nest air that are then swept away by the wind-driven flows in the mound.

Thus, respiratory gas exchange in the termite colony is a multiphase AC process, similar to the multiple phase AC function of the mammalian lung. The main difference between the two is the source and regularity of the AC energy driving exchange. In the lung, it is
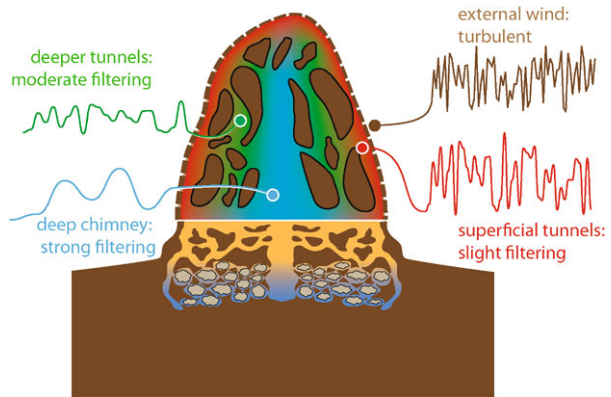
Fig. 4 The egress complex. (**a**) A plaster cast of a small egress complex taken at the top of a mound. (**b**) A partially exposed plaster cast of the surface conduits and egress complexes emerging from them. The *white dashed line* indicates the original surface of the mound. (**c**) A view of the inside surface of a surface conduit indicating numerous roots of egress complexes. (**d**) An egress complex appears on the mound surface as a patch of new build. (**e**) The underside of the patch in (**d**) indicates the spongy build ramifying through the patch and the underlying root of the egress complex. **ec**: egress complex; **rec**: root of egress complex; **sec**: surface of egress complex; **sc**: surface conduit
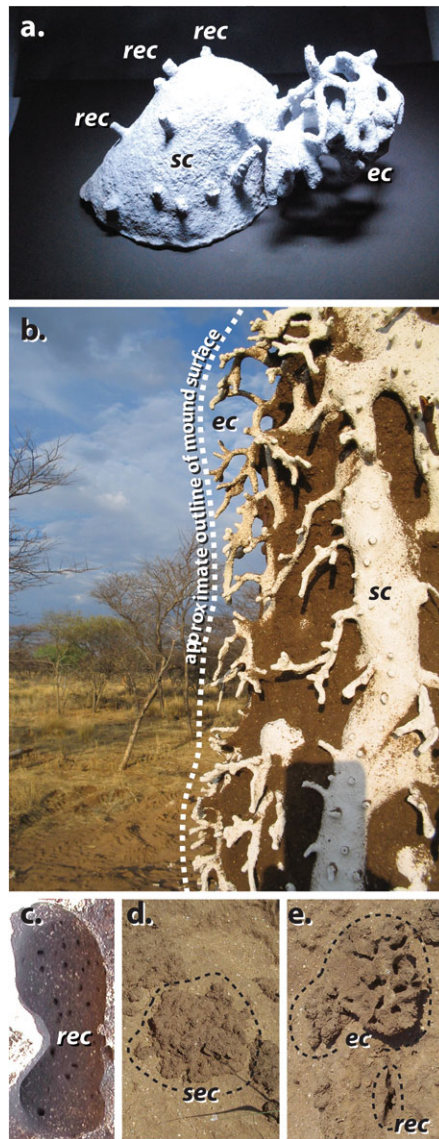
narrow-band cyclical contraction of respiratory muscle. In the termite mound, it is broad-spectrum turbulent wind. Just as in the lung, this complicated mechanism is supported by a complicated structure.

With that introduction, swarm cognition among termites can now be put into its proper context, from which two germane questions arise. First, how do termites *en masse* know how to build such a sophisticated structure? Second, how do they maintain the mound in the face of perturbations to its structure?

Fig. 5 Schematic of filtering
mechanism in the *Macrotermes*
mound. Details in text

deeper tunnels:
moderate filtering

external wind:
turbulent

deep chimney:
strong filtering

superficial tunnels:
slight filtering

3 How do termites build mounds?

The mound's complex function rests upon two salient structural features: the mound's surface porosity, and a particular distribution and orientation of tunnel sizes in the reticulum, specifically, large tunnels in the mound center grading into the small egress tunnels at the mound surface. Both arise through the mound being essentially a soil conveyor, with a net movement of soil from deep in the mound to the surface. As a consequence, voids open in the center as soil is removed and conveyed to the growing surface. The longer a location serves as a source for soil, the larger will be the voids that open there. Over time, the characteristic distribution of void space in the mound will emerge.

Soil movement occurs through a "bucket-brigade" mechanism. An individual termite will convey a pellet of soil just a few millimeters, but this pellet can be taken up by another termite and moved further, and then by another and so on. Using soil marked by polystyrene beads, we estimate that soil moves about 65 cm over a period of roughly six months. With this method, we have also established that soil conveyed to the surface can originate from sources as deep as the nest itself, a distance of roughly two meters.

The movements of soil through the mound are substantial, averaging about 250 kg dry mass per year. Nearly all of this occurs during the rainy season, and it is largely motivated by the need to export excess water that percolates into the nest from the torrential rainfalls that occur then. When termites move water, they usually do so in the form of wet soil, and water accounts for as much as a third of the mass of transported soil. Termites tend to move water and soil from wet localities to dryer ones, making the mound not just a soil conveyor, but a water conveyor as well. This too is substantial, conveying water to the surface at an export rate of about 125 liters of liquid water per year.

Swarm cognition enters into these movements of water and soil, and it occurs at two levels of organization, local and global. At the local level is the well-known process of stigmergy, whereby deposition of soil by one termite elicits deposition of soil by another, mediated by a putative "cement pheromone" laid down when soil is deposited (Grassé 1959). This drives an autocatalytic process, known as stigmergic building, which produces a characteristic suite of structures, ranging from simple pillars and walls to a complex space-filling reticulum known as the spongy build (Fig. 6). Stigmergic building frequently occurs in the context of mound repair, where its ultimate outcome is backfilling of the spongy build to form a solid plug (see below).

Stigmergic building produces focal building, conveying soil from a wide area to a point (Grassé 1959; Courtois and Heymans 1991; Bonabeau et al. 1999). Swarm cognition enters
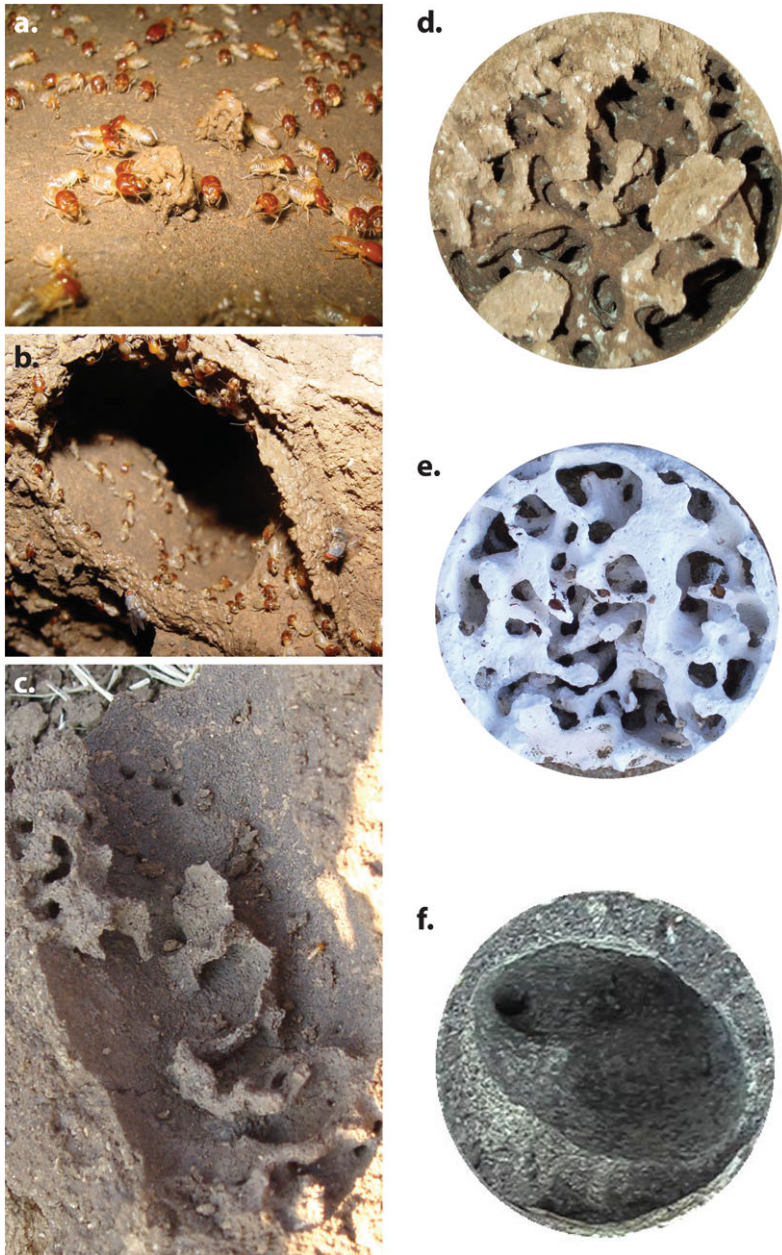
Fig. 6 The stages of stigmergic building by *Macrotermes* workers. (**a**) Punctate building which produces pillars. (**b**) Laminar building which produces linear walls. (**c**) Laminar building located in a surface conduit removed from the site of damage. (**d**) Space-filling spongy build built in a 100-mm PVC pipe implanted in the mound. (**e**) Plaster cast of spongy building within a PVC pipe. (**f**) View of remodeled build inside a perforated PVC pipe. The finely reticulated spongy build has been extensively remodeled into large smooth-walled spaces

because the swarm must "know" soil is to be conveyed to that point. The cognitive cues involved are provided by the stigmergic driver, usually assumed to be the cement pheromone. Stigmergic behavior by itself cannot explain the structure of the mound, however: that requires there to be a surface-oriented bias to the soil movements, which focally-biased stigmergic building cannot provide. For this, a larger-scale cognitive ability is required: to bias soil transport toward the surface, the swarm must somehow "know" where the mound surface is. This knowledge arises from global-scale maps of the interaction between mound and environment, which the swarm can then "read" to direct soil transport appropriately. From our work so far, it appears these maps have at least two dimensions.

The first dimension involves water, which biases soil movements upward, from nest up into the mound. The mound is commonly dryer than the nest, and the tendency of termites to convey soil and water from wetter areas to dryer areas will produce a net upward movement of soil. The bucket-brigade dynamic mentioned earlier means that this process will be autocatalytic: as a dry patch is moistened by the movement of wet soil into it, the dry patch converts from a net sink for water to being a source that will contribute water to another dry patch further on. This process is manifest during the transition from the dry season to the rainy season, as a rising wave of moisture that progresses up into the mound from the nest below.

The second dimension biases soil movement toward the mound surface and is more complex. The cue that termites follow in this circumstance is a gradient in the AC perturbations of the mound atmosphere brought about by turbulent wind. AC perturbations are intense toward the surface but are damped toward the center of the mound (Fig. 5). Termites are largely indifferent to steady levels of atmospheric components such as CO_2 concentration or water vapor partial pressure, but they are strongly motivated by *changes* of these quantities. In other words, individual termites are transducers of AC information about their environments, but tend to filter out DC information.

When presented with an AC perturbation, the individuals within a termite swarm do one of two things (Fig. 7). Some individuals rush toward the source of the perturbation:
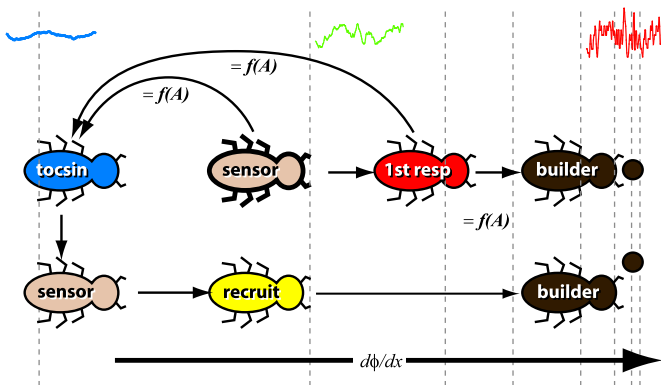

Fig. 7 Model of global swarm cognition. The default state of termites is "sensor", capable of sensing and responding to transient perturbations in the local environment that are characterized by time dependent fluctuations of amplitude, $f(A)$, and frequency, ϕ. When sensor termites detect a transient that exceeds a critical amplitude and frequency, they convert to one of two modes: 1st responders or tocsins. Tocsins vicariously inform other sensor termites there has been a perturbation, which become recruits. As termites approach regions of intense transient perturbation, they convert to builders, initiating stigmergic building, described in Fig. 6. Once a site of stigmergic building is initiated, termites' activities are driven by local cognitive information outlined in Fig. 5

Fig. 8 Effect of transients on initiating stigmergic building. (**a**) Stigmergic pillar build atop a soil plug. Note the yellow polystyrene beads embedded in the build. (**b**) Recovery of beads from stigmergic build when termites are exposed to intense environmental transients compared to lighter environmental transients
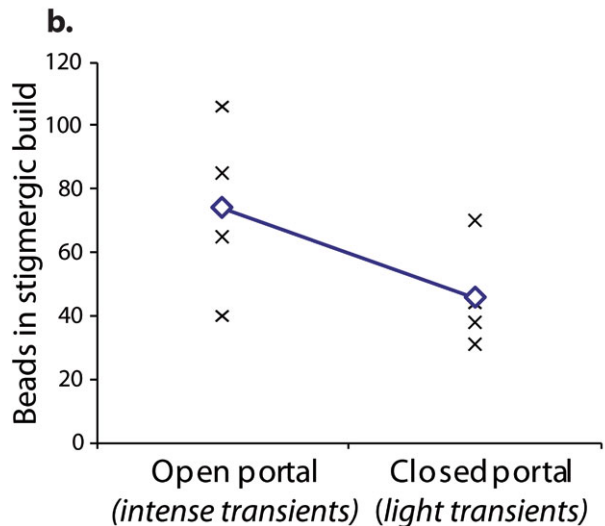
these we call "first responders." Other individuals rush away from the source: these we call "tocsins." The tocsins' main task is recruitment of other termites, essentially informing them vicariously of the perturbation, who then themselves tend to proceed *en masse* toward the source of the perturbation. Termites appear to switch between these roles, but the net result is a statistical bias of termites' movements toward the site of perturbation. Building comes into the picture because exposure to AC perturbations also increases the likelihood that termite swarms will initiate stigmergic building (Fig. 8). Once initiated, stigmergic building becomes autocatalytic.

When placed in the context of the mound's AC filtering of turbulent wind energy, activation and building will be biased to the mound surface (where AC perturbations are strong and broad band), and away from the mound interior (where AC perturbations are weak and filtered). When stigmergic building is activated at the surface conduits, the result is an egress complex. Deeper in the mound, the gradient in AC perturbation biases the bucket brigade toward the surface. Thus, the distribution of AC perturbation within the mound serves as a sort of cognitive map that uses the mound's interaction with the temporal dimension of turbulent wind to inform termite swarms of direction and orientation with respect to the mound surface. In this sense, the mound's role in swarm cognition is akin to the role played by the

optical structures of the eye: interfaces that mold a feature of the physical world—light in the one case, turbulent wind energy in the other—into a form that the sensitive units of cognition can use to read a cognitive representation of the outside world. There is a sense, however, in which the mound itself forms a cognitive map, because the mound is a dynamic interpretive structure that represents the innumerable negotiations among the cognitive agents and the interpretive structures they build, somewhat akin to the self-organization of the visual cortex into complex interwoven striations that represent visual fields. No matter how we interpret the mound, its origin underscores the importance of the environmental dimension in cognition: termite swarm cognition is only evident in the context of the mound and its interaction with turbulent wind.

4 How do termites maintain mounds?

Mound building is a rainy season phenomenon, because it is essentially enabled by water: excess water percolating into the nest brings termites up into the mound where they otherwise might not venture. It also brings termite swarms into areas where they are more likely to experience the strong AC perturbations that trigger stigmergic building. However, termite mounds are always susceptible to damage, whether from erosion, attack by predators such as aardvarks, or from catastrophic collapse. This compromises mound function, which the termites restore through programs of mound repair and restoration. Unlike mound building, mound repair can occur at any time of the year, even when it is very dry. This presents the termite colony another suite of cognitive problems: how does the colony become informed that the mound has suffered damage, how does the termite swarm know where the damage has been done, and how does the swarm come to concentrate its repair activities there? Here, the mound's role as a mediator of swarm cognition becomes more evident.

Damage to the mound surface substantially alters the distribution of AC perturbation in the mound and nest (Fig. 9). Specifically, a breach in the surface acts as a portal for admission of high-frequency AC wind energy into regions of the mound where it normally would have been filtered out. These AC perturbations can extend even into the nest. Thus, the recruitment and triggering events that normally would occur only near the surface of the intact mound may now occur deeper. One of the remarkable features of repair is the initiation of numerous sites of stigmergic building throughout the mound, reflecting the higher likelihood that termites will encounter a transient perturbation large enough to trigger stigmergic building. Each focus of stigmergic building therefore represents a "hypothesis" of an assemblage of termites for where repair efforts are called for. Over time, a competition arises between these scattered foci of stigmergic building, with the sites where AC perturbations are stronger competing for workers against sites where AC perturbations are weaker. The winner will inevitably be at the site of the damage because it is there that the AC perturbations are strongest. As this site "wins", more and more workers will attend the site, focusing stigmergic building there until the breach is plugged. At this point, the AC perturbations are once again blocked off, workers dissipate and building activity declines. After the breach in the mound is plugged, the abandoned sites are gradually dismantled and the tunnels remodeled to their original smooth surface. This process can take weeks to months, even spanning multiple rainy seasons.

This process is remarkably similar to the assembly of cognitive maps in the brain. Sensing agents detect a change of state without "knowing" many details on what the change of state actually is. There follows the generation of numerous "hypotheses" about what the change of state is. There is then a "debate" between these competing hypotheses until one persuades enough agents that it has "got it right", at which point the "incorrect" hypotheses are abandoned and the most "persuasive" hypothesis prevails.

Fig. 9 (Color online) Sequence of events during mound repair. (**a**) Normal distribution of transient perturbation in nest and mound. *Red* indicates intense transient perturbation, green indicates moderate transient perturbation, blue indicates mild transient perturbation. (**b**) A breach in the mound perturbs the perturbation field, with a focus at the breach. (**c**) The distorted perturbation field provides vector patch for termites to follow. (**d**) Stigmergic building is initiated throughout the mound, most intensely near the breach. (**e**) Competition between multiple stigmergic building sites is resolved when sites near the breach "win." The perturbation field then returns to normal (**a**)
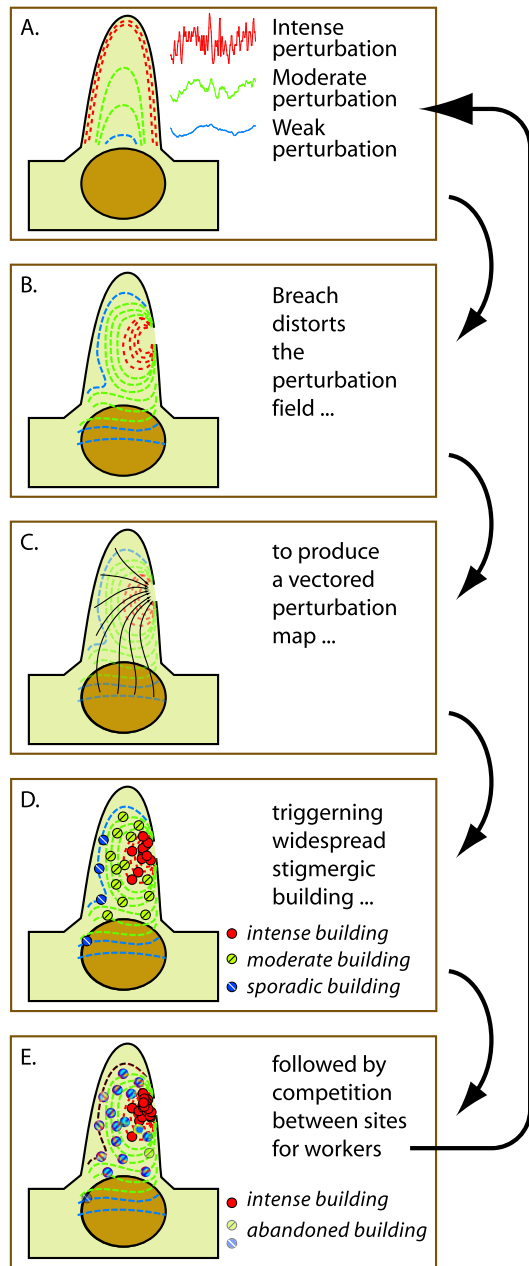
5 Water as an organizer of swarm behavior

One surprising aspect of termite swarm behavior that has emerged from our natural history approach is a significant role for water in organizing and directing building behavior. Even more interesting, we have found significant species differences that correlate to large scale species differences in mound and nest architecture.

These species differences become evident in laboratory experiments where termites are allowed to interact with soil pellets provided them, often in the context of a choice between two soil pellets that differ in some attribute, like moisture. Termites' movements can be followed using videography and image analysis. Soil movements can be followed by seeding the pellets with unexpanded polystyrene beads, which termites will move as they do soil grains. Water movements can be followed using non-toxic fluorescein dye, which can label termites that imbibe water from soil and move it around (Turner 2009a, 2009b, 2009c). A video showing this method is available as Video 1—Termite drinkers—in the online supplementary material.

When given soil as a source for stigmergic building, both species show a marked preference for wet soil as a source (Fig. 10). Of the two, *M natalensis* is the more avid stigmergic builder. Termites will also transport soil away from a pellet: here, *M michaelseni* appear to distribute soil more widely. *M michaelseni* also scatter soil more widely from wet soil than they do from damp soil, while *M natalensis* scatters soil indifferently from either wet or damp sources. In addition, *M michaelseni* imparts a distinct bias to its scattering, tending to move soil strongly from wet to damp soils. *M natalensis*, in contrast, shows no such bias: it moves soil as much from damp to wet soil as it does from wet to damp soil (Fig. 10).

Another interesting species difference involves the putative cement pheromone that is widely thought to organize stigmergic building. When *M natalensis* workers are presented with a soil pellet from an active site of stigmergic building (fresh build), or a soil pellet made from "neutral build" (soil from a termite mound that has been removed and exposed to the weather for several months), they show a marked and immediate preference for the fresh build (Fig. 11). *M michaelseni* workers, in contrast, show no such preference. This interesting result indicates that cement pheromone may drive stigmergic building more strongly in *M natalensis* workers than it does in *M michaelseni* workers. Indeed, the results question whether *M michaelseni* has a cement pheromone at all: water appears to be the stronger driver of soil movements in this species.

Finally, termite swarms appear to have a complex internal water distribution economy. When they encounter a patch of wet soil, termites commonly drink from it. In some instances, they imbibe substantial amounts of water, imbibing nearly half their initial weight of water. This imbibed water can then be distributed to other termites, usually in the aftermath of a prolonged ritual of grooming and begging by the termites receiving the water largesse. This process can be followed by marking the water with fluorescein dye. When termites imbibe fluorescein-labeled water, they glow brightly under UV light. Water sharing is evident by introducing fluorescein-labeled termites into a swarm of unlabeled termites, and then counting the incidence of newly fluorescent termites (Fig. 12).This behavior is also depicted in Video 1—Termite drinkers—that is available in the on-line supplementary material. Both species take up water quite rapidly, but *M michaelseni* distributes water much more quickly and more broadly to other termites than *M natalensis* does. On average, *M michaelseni* will share their water loads with about three other termites. *M natalensis* workers share water with two other workers on average.

These behavioral differences correlate with the differences in mound architecture. Specifically, building behavior of *M michaelseni* appears to be more strongly driven by water, and has a stronger tendency to move soil and water along gradients from wet to dry. Building behavior of *M natalensis*, in contrast, appears to be more confined by a greater reliance on cement pheromone to organize building. The taller mound of *M michaelseni* may therefore be accounted by its being a more "exuberant builder", organized more strongly by large scale gradients in soil moisture than *M natalensis* swarms are. In *M natalensis* swarms, for their

Fig. 10 (Color online) Water as an organizer of soil movements by termite swarms. (*Top panel*) Mobilization of beads into stigmergic build only. (*Middle panel*) Dispersal of beads from soil pellets that differ in moisture content. "Wet" soil refers to a soil pellet with water added to the point of puddling, roughly 30% by weight. "Damp" soil refers to a soil pellet with just sufficient water added to make the pellet cohere, typically about 3% by weight. (*Bottom panel*) Movement of beads between soils of different moisture contents. *Open diamonds*: average of all; *Red triangles*: *M natalensis* swarms only; *Magenta squares*: *M michaelseni* only
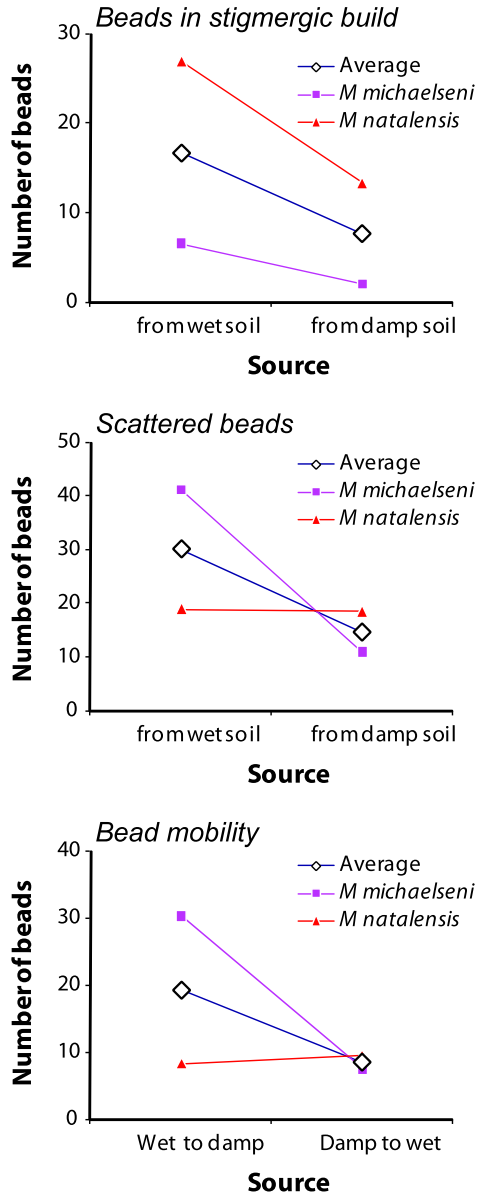
part, the building behavior is more strongly stigmergic (and therefore focal) in nature. Because stigmergic building is self-limiting, *M natalensis* are therefore the more "restrained" builders, therefore producing smaller structures.

6 Elements of termite swarm cognition

From these and other results, we have formulated a rough working model of swarm cognition among termites. At its base are three fundamental sensory modalities that feed information
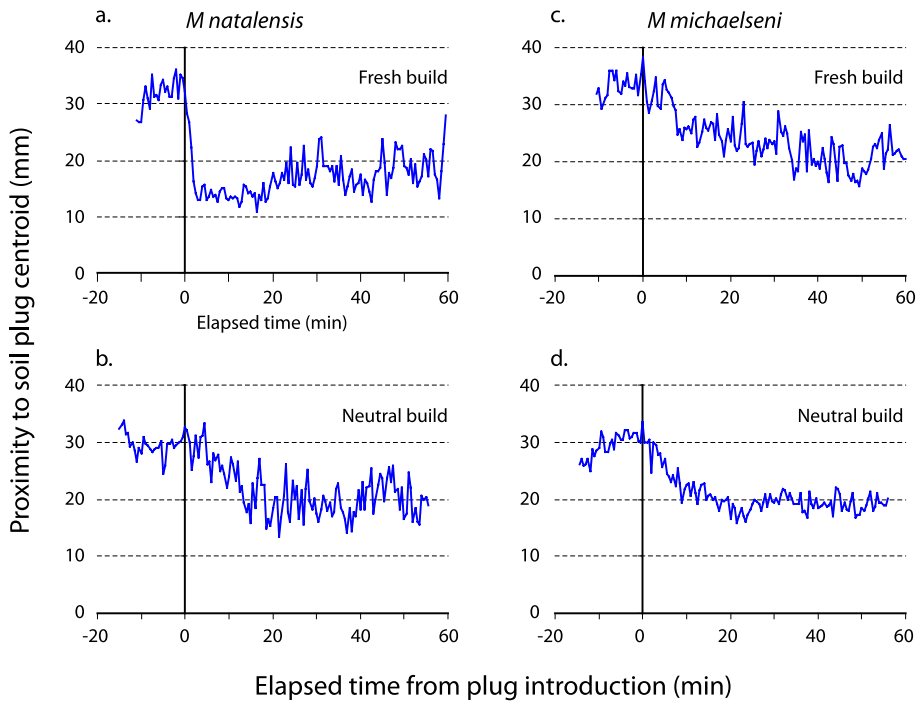
Fig. 11 Response of different species to putative cement pheromone. Experiment measured the proximity of worker termites to the centroid of a 30 mm diameter soil pellet. Pellets were made either from fresh build, removed immediately prior to the experiment from an active site of stigmergic building, or from "neutral build", soil removed from a termite mound that had leached for several months. Time zero is the introduction of the pellet to the swarm. *M natalensis* workers gravitate immediately to fresh build, but migrate only slowly to moist neutral build. *M michaelseni* workers are indifferent to whether the soil pellet is fresh build or neutral build

about the physical and social environment to individual termite brains. The first modality is tactile inputs that arise through physical contact between termites, or between termites and physical objects in the environment. These can include the self-constructed environment of the mound. Second, termites are sensitive to fluctuations in local conditions, such as local CO_2 concentrations, humidity and air currents. Finally, there is a rich medium of chemical communication between termites, mediated mostly by pheromones. These can be air-borne chemicals or chemicals laid down by other termites. There is no visual cognition: *Macrotermes* workers are blind.

From these sensory channels, the termite compiles a cognitive representation of its local world. In addition to these cognitive inputs, internal drives may also impel termites to certain behaviors. We know, for example, that termites deprived of water for a few hours will avidly seek out wet soil when it appears, so there is a thirst driver in operation. Termites normally live in a rich cognitive world of tactile, environmental and chemical information. Each of these modalities can shape swarm behavior in different ways. Tactile cues, for example, elicit behaviors like edge following or clustering, a peculiar state where termites seek each other out and form into dense assemblages. Environmental perturbations tilt swarm behaviors toward recruitment, as described above. The pheromonal channel biases swarm behavior toward stigmergic building, queen cell construction and trail following. Depend-

Fig. 12 Water sharing in termite swarms. Distribution of water is measured by distribution of fluorescein dye. Five water-sated termites ("sharers") are introduced to 25 thirsty termites. If water is transferred from a sharer to a thirsty termite, the latter becomes an "imbiber", which is detected by when it glows under UV light. The number of fluorescing termites is the sum of the number of initial sharers and imbibers. A video of water imbibing and sharing is available as Video 1 in the online supplemental material
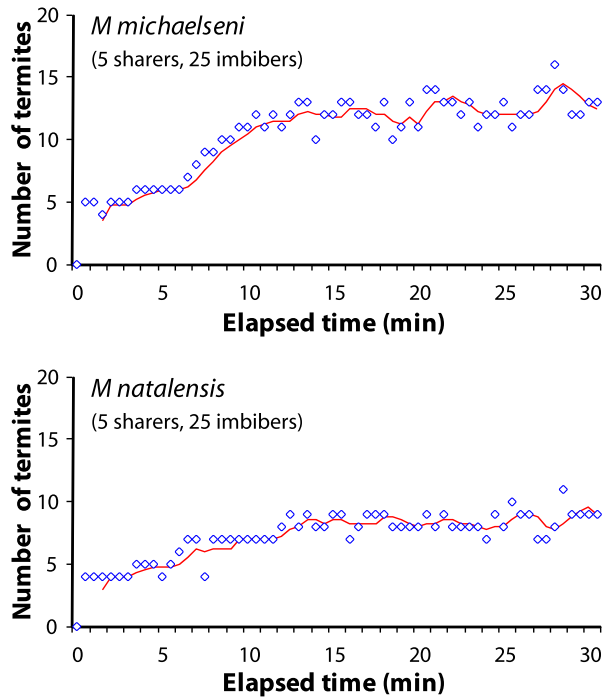
ing upon the particular mix of sensory information coming in, termite swarms may tend toward one or the other of these swarm behaviors. In the initial stages of mound repair, for example, termites face a mix of tactile, environmental and chemical signals. This produces the confused initial response, whereby some swarms initiate stigmergic building, only to be diverted from this from time to time by strong environmental perturbations. Ambiguity declines in the later stages of repair, where pheromonal signals dominate and the swarm is overwhelmingly directed by stigmergic building.

7 Swarm cognitive disorders?

A well-functioning cognitive system should provide a reasonably faithful mental representation of the real world. Real cognitive systems sometimes fail in this, and the result is a cognitive disorder, such as schizophrenia. In brains, these appear to arise for the most part from some disregulation of the various cognitive sub-systems of the brain: visual, auditory, interpretive, mnemonic and so forth.

If there is, in fact, such a thing as swarm cognition, it follows that there should also be swarm cognitive disorders. We have identified several instances of anomalous swarm behaviors in termites that we believe qualify as swarm cognitive disorders. These could serve as useful experimental probes into the diffuse process of swarm cognition.
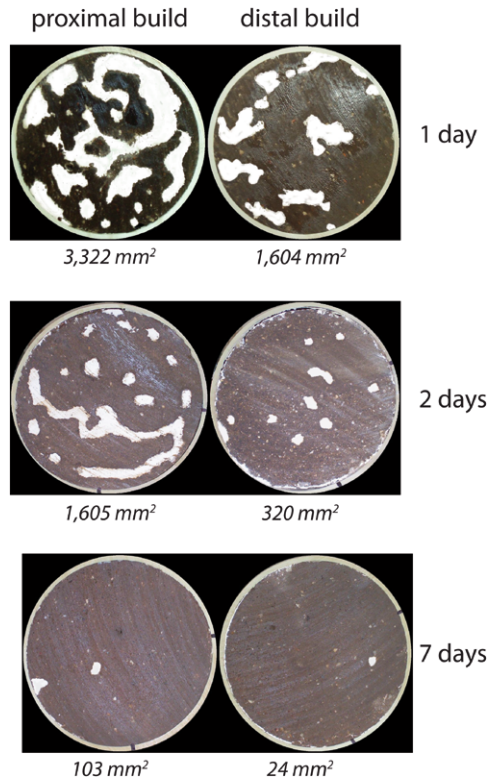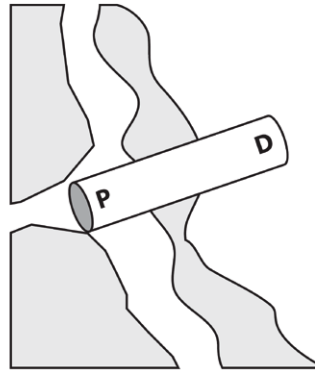
7.1 Anomalous plug formation

The first example is driven by a disordered representation of the progress of mound repair. In normal mound repair, the resolution of the many competing "hypotheses" outlined above

concentrates stigmergic building at the site of damage. This culminates in the production of a plug that seals the breach, which marks the end of the stigmergic building phase of repair.

Stigmergic building can be induced in artificial as well as natural situations. One technique that we have used is to place a 100-mm diameter PVC pipe into the mound, open at the implanted end and capped at the outside end (Fig. 13). Termites will avidly build in this situation, producing an advancing front of spongy build progressing up the pipe. At some point, a plug is formed at the front's distal surface, as occurs in natural repair. The putative

Fig. 13 Sequence of stigmergic building in a 4″ PVC pipe implanted into a termite mound. *Top panel* indicates placement of PVC pipe in the mound. The pipe's proximal end (P) is open, giving worker termites access to the pipe. The pipe's distal end (D) is capped. Bottom panels are photographic of spongy build at 1, 2 and 7 days. Cross-section areas of void space are given *below each photograph*. The culmination of stigmergic building is complete packing of the pipe with soil
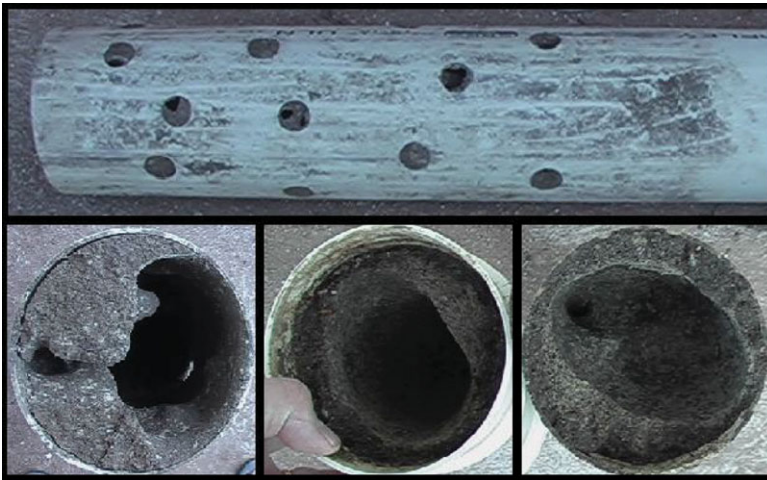
proximal build   distal build

3,322 mm²   1,604 mm²   1 day

1,605 mm²   320 mm²   2 days

103 mm²   24 mm²   7 days

Fig. 14 Remodeling in a perforated PVC pipe. (*Top panel*) Side view of the perforated PVC pipe described in the text. Access holes are visible on the labeled perforations. (*Bottom panels*) Three views of the remodeled plug inside a perforated PVC pipe. Termites building in the perforated pipe have made the normal transition from stigmergic building and plug formation to remodeling the soil, opening large voids similar to the mound reticulum. Contrast with the course of building in the non-perforated pipe sections in Fig. 13. **D**: distal end of pipe; **P**: proximal end of pipe; **pf**: perforations; **vo**: excavated void spaces; **pl**: remaining solid plug

cognitive disorder becomes evident in the subsequent course of stigmergic building within the pipe. In normal mound repair, the plug produced is only a few centimeters deep, and the cessation of stigmergic building and the initiation of remodeling takes place within a few hours. In the pipe, however, stigmergic building continues for several days, culminating in the pipe becoming completely packed with soil (Fig. 13). In short, the termites produce a "plug" that extends the entire length of the pipe, usually half a meter in our experiments. This anomalous result follows from a failure of the swarm to make the transition from stigmergic building phase to remodeling. When numerous holes are drilled in the pipe wall, however, the transition to remodeling occurs normally (Fig. 14), appearing and numerous large voids that have opened within the soil packed into the pipe.

The anomalous behavior results from a disruption of the cognitive cues that terminate the stigmergic building phase. Let us assume that the intensity of stigmergic building is proportional to the number of workers engaged in stigmergic building, which itself is a balance between recruitment of workers to stigmergic building, and the reversion of workers from stigmergic building to other activities. Recruitment is effected in two ways: by encountering a transient perturbation sufficiently intense to trigger the conversion of a worker to a builder, or by encountering a local concentration of cement pheromone sufficiently high to stimulate stigmergic building. In the early stages of stigmergic building, pheromone concentration is a weak recruiter, because few workers are involved. Transient perturbations, in contrast, are initially strong, and this is the principal driver of stigmergic building then. As numbers of builders (and pheromone deposition rates) increase, recruitment shifts primarily to being pheromone-driven, and becomes autocatalytic and self-sustaining.

For its part, pheromone concentration is the balance between pheromone deposition rate and its dissipation rate. Deposition rate is a direct function of the number of workers engaged in stigmergic building, which is itself determined by the balance between recruitment and reversion. Dissipation of the pheromone can come about in two ways, either through chemical

decay or through dispersal. Chemical decay is peculiar to the particular pheromone: some may degrade at faster rates than others. In some instances, when water is the "pheromone" driving stigmergic building, as appears to be the case for *M michaelseni,* the decay term is *null.* Dispersal is determined by the structure of the spongy build, in particular the connectivity of the build's void space to the larger air space of the mound. Dispersal is lowered as the voids in the spongy build become smaller, more tortuous and more isolated from the larger air spaces of the mound.

This conceptual model helps clarify the cognitive processes behind the normal course of stigmergic building, as well as how these cognitive processes can become disordered in the pipe. In normal mound repair, recruitment is either transient-triggered, or pheromone-triggered. Prior to plug formation, transient triggering is particularly intense in the distal parts of the build, so the most intense stigmergic building occurs there. It also means that pheromone-triggered recruitment will be most intense there.

As the plug is formed, transient-triggered recruitment declines, leaving only pheromone-mediated recruitment to drive stigmergic building. As distal soil deposition proceeds, it will shrink the distal voids in the spongy build, restricting pheromone dispersal there, which drives up local pheromone concentration, and which further enhances distal soil deposition. This autocatalytic process produces backfilling behind the plug, deepening it until the backfilling reaches the mound's larger air spaces, where pheromone can disperse more easily. At this point, plug formation stops and the swarm can proceed to remodeling. Thus, termite swarms "know" when plug formation is finished because the interaction of building with structure provides the swarm a cognitive representation of the plug's completion.

When swarms build in a pipe, this cognitive representation is distorted, because the pipe now interferes with the dispersal aspect of the cognitive cues that inform the swarm when plug formation is "done." Stigmergic backfilling thus continues for much longer than it ordinarily would, packing the pipe solidly with soil, essentially producing an anomalously thick plug. This also explains why plug formation and the transition to remodeling occur normally if the pipe has had numerous holes drilled in the side (Fig. 14). Pheromone dispersal is no longer compromised, restoring the cues that tell the swarm when plug formation is complete.

7.2 Swarm aphasia

Termite swarms are organized through a complex language of tactile and chemical signals between individual members of the swarm. These drive the process of recruitment in response to transient perturbation of the environment, as might occur following mound injury, as described above. An individual termite can either experience such a perturbation directly, or experience it vicariously, being informed of it by other termites.

This process can be easily observed in vitro. Termites are placed in a chamber consisting of two "lanes" joined by a common well (Fig. 15). Air is precisely metered through both lanes. Introducing a short pulse of CO_2 into one lane exposes the termites in that lane directly to a transient perturbation. Termites in the other lane cannot directly sense the perturbation, however, but can be informed of it indirectly by tocsins. Recruitment is indicated by movement of termites in this second lane.

As swarm density increases, there appears to be a breakdown of the language that drives recruitment, a kind of crowding-induced swarm aphasia (Fig. 15). When the swarm contains 50 termites, a transient pulse quickly activates termites in the directly exposed lane, and there follows a vigorous recruitment in the vicariously sensed lane. When the swarm is increased to 75 termites, activation in the directly exposed lane is still vigorous, but now recruitment
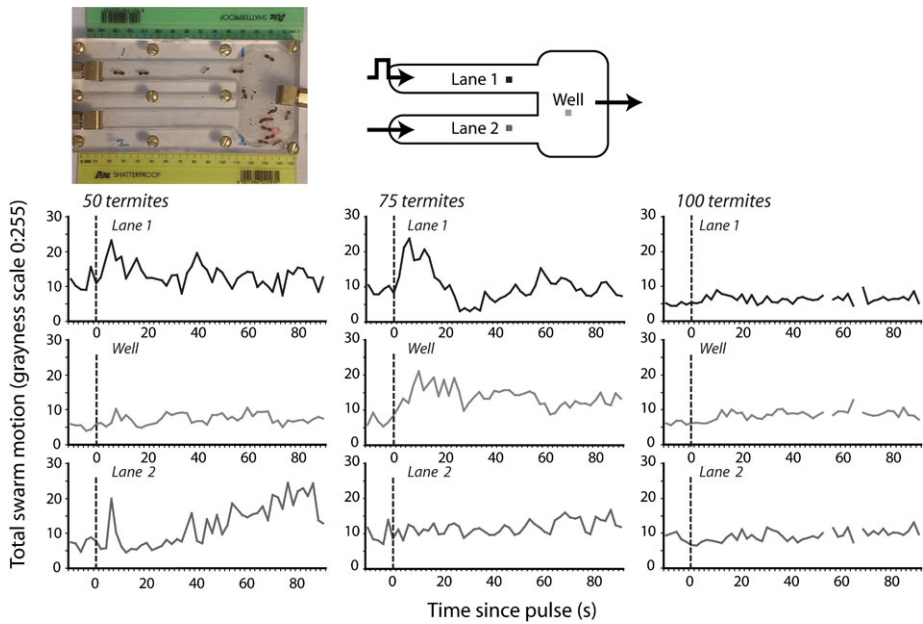
Fig. 15 Density induced swarm aphasia. Top panels depict the apparatus used to partition direct responsiveness to perturbations from indirect recruitment. *Graphs* depict total swarm motion in the two lanes and the well connecting them. Total swarm motion is measured from image analysis of video recordings of the respective regions of the apparatus. It is assessed by measuring the change of position of termites at 100 ms intervals, and so represents the collective motion of the swarm. Total swarm motion is measured as a grayness value that ranges from 0 to 255. *Left graphs* represent motion at low swarm density, *middle graphs* represent motion at intermediate swarm density and *right graphs* depict motion at high swarm density. A video of density-induced swarm aphasia is available as Video 2 in the online supplemental material

in the vicariously sensed lane is poor. Recruitment still occurs in the well, where termite densities are lower. With a 100 termite swarm, all termites are insensitive to the perturbation, even when it is experienced directly. High density appears not only to compromise the direct language between termites that produces recruitment, but also to desensitize the termites to higher-order cognitive cues such as transient perturbations of their environment.

The model for swarm cognition outlined above provides a useful interpretation of this apparent swarm aphasia. If termite brains have a capacity limitation on processing sensory input, it follows that increasing intensity in one modality will crowd out other modalities. As swarm density increases, one can expect the inputs through the tactile channel to increase, perhaps to the point where the termites become insensitive to other inputs. Thus, termites in intermediate density swarms are resistant to recruitment, even if they are directly sensitive to a perturbation stimulus: the swarm is responsive, but partly aphasic. In high density swarms, even the receptivity to environmental perturbations is diminished, and the swarm becomes completely aphasic. A video of this transition to crowd-induced aphasia is provided in Video 2—A swarm cognitive trap—in the on-line supplemental material (Turner 2009a, 2009b, 2009c).

7.3 Signal persistence/habituation mismatching

The mound is an AC filtering device for turbulent wind, largely because it is built by creatures whose cognitive systems are tuned AC devices themselves. In more conventional

terms, termites habituate to sensory stimuli, so that termites become less responsive to a particular level of sensory input, say that arising from a particular concentration of CO_2, the longer they are exposed to it. The response to a change of CO_2 concentration, in contrast, is much more intense.

It follows that there must be some degree of matching between the time domains of transient environmental stimuli and habituation. The mathematics behind such matching is complex, but it is analogous to the well-known phenomenon of impedance-matching in electrical and acoustical systems.

In a nutshell, the habituation to a particular sensory stimulus is quantified by some time constant of decay. Any activity stimulated by a step change of the sensed property, say an increase of CO_2 concentration, will therefore decline with time. Transient stimuli, for their part, also have a time domain that can be described as a frequency of variation. To be responsive, there must be good matching between the time domains of sensory habituation and environmental stimuli. When the period of a transient environmental stimulus is less than the receiver's habituation time, the system will be responsive. When the transient stimulus period is longer than the habituation time, the system's responsiveness is diminished. To reiterate, this is why mound building is a surface phenomenon: the high frequency (short period) components of turbulent winds are relatively unfiltered and so have periods much less than the termites' habituation times: in short, there is good impedance matching between termite and environment. Deep in the mound, where only the low frequencies have been admitted, periods of transient stimuli are longer than the habituation times, so that these are essentially invisible to the termites. Impedance matching between cognitive system and environment is poor there.

The effects of mismatches in time domains can be modeled in an agent-based simulation platform such as NetLogo. Snapshots of one such simulation is depicted in Fig. 16 (Turner 2009a, 2009b, 2009c). A video of these simulations is available as Video 3—Cognitive trap demo—in the supplemental online material. Here, agents lay down attractive pheromone trails whose persistence times can be altered through adjustments of diffusion rate and evaporation rate. This changes the time domain of the environmental stimulus. In this simulation, the termites' habituation time can also be altered, essentially by changing the strength of attraction to pheromone.

Fig. 16 (Color online) Emergence of a simulated cognitive trap induced by a mismatch between signal persistence (left to right) and habituation time (top to bottom). Pheromone concentration is indicated by *shades of green*. The darker the *green*, the greater the concentration. Termites are colored *red*. The four panels represent snapshots from an agent-based simulation of swarm behavior in which persistence of pheromone can be altered by changing its diffusion and evaporation rates. The modeling platform is NetLogo. A video of this simulation is available as Video 3 in the online supplemental material
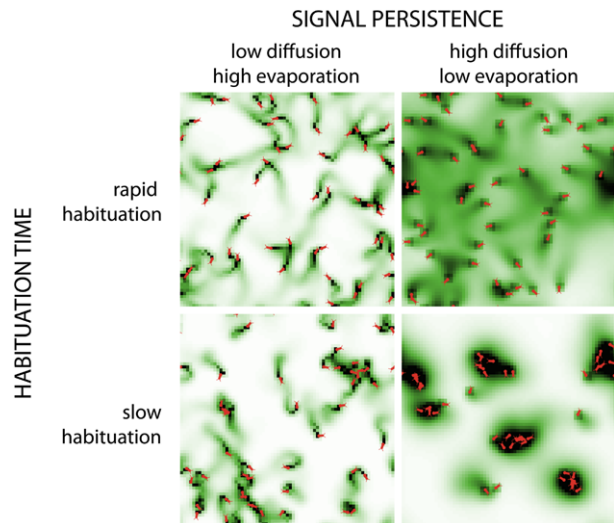
When habituation is rapid (that is, the habituation time constant is short), agents move about more or less at random, irrespective of whether the persistence of the pheromone is long or short (Fig. 16). This is because pheromone attractiveness very quickly "wears off" in rapidly habituating termites. With long habituation times, though, termite swarms enter into a self-perpetuating cognitive trap. Once a termite has entered a pheromone cloud, it tends to stay there, because the attractive power of the pheromone persists, i.e., it does not "wear off". The trap becomes self-perpetuating because termites deposit more pheromone as long as they reside within the cloud. Thus, the effect of a mismatch in signal persistence/sensory habituation is to drive termites into a "cognitive trap" from which they cannot escape. It is the swarm equivalent of an obsessive/compulsive disorder in human cognition.

8 Does swarm cognition exist?

At its root, cognition is a means of creating a representation of an environment in which an organism lives. This representation must be accessible to the organism in such a way that it can be interpreted, and acted upon appropriately. The representation so created should also map the environment with reasonable fidelity. To do so, cognitive systems require a minimal set of elements. Among these are sensors, for transducing whatever physical signature of the environment is being mapped (patterns of light, sound, pressure, chemicals, etc.) into some form of information that is accessible to the cognitive agents. These devices can either sense the environment directly, as photosensors do; or vicariously, as simple cells of the primary visual cortex, or cells in the lateral geniculate nuclei, do. There must also be a physical interface between the sensors and the environment, such as the structures of the optical eye (cornea, iris, lens, vitreous body and aqueous humor) that focus light information into a usable image. Finally, cognitive systems seem organized into hierarchies, so that multiple incomplete mental representations are formed between initial sensation and ultimate cognitive map. The information processing structures of the retina, lateral geniculate nuclei, and visual cortex are examples of this.

Brains and sensory systems are the usual context for our thinking about cognitive systems, but there is no inherent reason why cognitive systems need be circumscribed in this way. Life occurs at multiple scales of organization, ranging from cell to organism to superorganism. If cognition is useful for one level of organization, as it clearly is for organisms, it is difficult to argue that cognition would not be useful, or possible, at higher organizational levels as well. So by simple logic alone, swarm cognition is not only imaginable, it should be likely.

In this article, I have argued that there exists a superorganismal cognition that operates at the level of the termite colony and its affiliated structures. My case is largely analogical. The mound, for example, is a physical interface between the colony and an aspect of its environment that is important for the colony to know—the interaction with turbulent wind. In this instance, the mound serves the same function as the optical structures of the eye, even though the nature of the images are radically different in the two: a two-dimensional light image in the one case, and a three-dimensional map of turbulent perturbations in the other. Similarities also exist in how the respective systems solve a cognitive problem. Reconstructing 3D information from the 2D image projected onto the retinas often requires the resolution of conflicting information from the two eyes, for example, and this often involves competition between multiple "hypotheses" constructed by the various centers of the brain on what the "true" representation is. These are then resolved through a competitive process of inhibition and facilitation. We see something similar in the termite mound following perturbation to its structure, where the swarm poses multiple "hypotheses" about the location of

damage, which are then resolved through a competitive interchange of information between subsets of the swarm. Finally, there is a component of memory, as Passino et al. (2008) indicate, that is involved in honeybee swarm cognition in the context of choosing among various candidate sites for the swarm to inhabit. Similarly, one can say with some confidence that collective memory, both long-term and short-term, resides in termite swarms, although these are likely to be embodied in the structure of the mound, in transient structures that arise in the context of mound building and maintenance, and in the distributions of perturbation, water and pheromones.

It is possible to draw other analogies, but what seems to unite them all is that cognition involves much more than the interchange of information between cognitive agents. Rather, swarm cognition depends upon patterns of information exchange and processing between cognitive agents, and with the built structures that shape the functional interaction between agent and environment.

References

Aanen, D. K., Eggleton, P., Rouland-Lefèvre, C., Guldberg-Frøslev, T., Rosendahl, S., & Boomsma, J. J. (2002). The evolution of fungus-growing termites and their mutualistic fungal symbionts. *Proceedings of the National Academy of Sciences (USA)*, *99*(23), 14887–14892.

Agosti, D., & Johnson, N. F. (2005). Antbase. World Wide Web electronic publication. antbase.org, version (05/2005). Available at http://antbase.org/.

Batra, S. W. T., & Batra, L. R. (1967). The fungus gardens of insects. *Scientific American*, *217*, 112–120.

Batra, L. R., & Batra, S. W. T. (1979). Termite-fungus mutualism. In L. R. Batra (Ed.), *Insect–fungus symbiosis. Nutrition, mutualism and commensalism* (pp. 117–163). New York: Wiley.

Bechara, A. (2002). The neurology of social cognition. *Brain*, *125*, 1673–1675.

Bonabeau, E., Dorigo, M., & Theraulaz, G. (1999). *Swarm intelligence. From natural to artificial systems*. New York: Oxford University Press.

Collins, N. M. (1979). The nests of Macrotermes bellicosus (Smeathman) from Mokwa, Nigeria. *Insectes Sociaux*, *26*(3), 240–246.

Courtois, P. J., & Heymans, F. (1991). A simulation of the construction process of a termite nest. *Journal of Theoretical Biology*, *153*, 469–475.

Dangerfield, J. M., McCarthy, T. S., & Ellery, W. N. (1998). The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology*, *14*, 507–520.

Darlington, J. P. E. C. (1985). The structure of mature mounds of the termite *Macrotermes michaelseni* in Kenya. *Insect Science and Its Application*, *6*(2), 149–156.

Darlington, J. P. E. C. (1986). The structure of mature mounds of the termite *Macrotermes michaelseni* in Kenya. *Insect Science and Its Application*, *6*, 149–156.

Darlington, J. P. E. C. (1990). Populations in nests of the termite *Macrotermes subhyalinus* in Kenya. *Insectes Sociaux*, *37*(2), 158–168.

Darlington, J. P. E. C. (1994). Nutrition and evolution in fungus-growing termites. In J. H. Hunt & C. A. Nalepa (Eds.), *Nourishment and evolution in insect societies* (pp. 105–130). Boulder: Westview Press.

Darlington, J. P. E. C., Zimmerman, P. R., Greenberg, J., Westberg, C., & Bakwin, P. (1997). Production of metabolic gases by nests of the termite *Macrotermes jeaneli* in Kenya. *Ecology Journal of Tropical*, *13*, 491–510.

Golley, F. B. (1993). *A history of the ecosystem concept in ecology*. New Haven: Yale University Press.

Grassé, P.-P. (1959). La reconstruction du nid et les coordinations inter-individuelles chez *Bellicositermes* et *Cubitermes* sp. La théorie de la stigmergie: Essai d'interprétationdu comportement des termites constructeurs. *Insectes Sociaux*, *6*, 41–80.

Harris, W. V. (1956). Termite mound building. *Insectes Sociaux*, *3*(2), 261–268.

Hutchins, E. (2000). *Cognition in the wild*. Cambridge: MIT Press.

Kandel, E. R., Schwartz, J. H., & Jessell, T. M. (Eds.) (1991). *Principles of neural science*. New York: Elsevier.

Krishna, K., & Weesner, F. (1969). *Biology of termites*. New York: Academic Press.

Lüscher, M. (1961). Air conditioned termite nests. *Scientific American*, *205*(1), 138–145.

Michener, C. D. (2000). *The bees of the world*. Baltimore: Johns Hopkins Press.

Millonas, M. M. (1994). Swarms, phase transitions, and collective intelligence. In C. G. Langton (Ed.), *Artificial life III* (pp. 417–445). Reading: Addison-Wesley.

Mitchell, W. (1977). Ecological effects of termite mounds. *Wild Rhodesia*, *14*, 11–14.

Moritz, R. F. A., & Southwick, E. E. (1992). *Bees as superorganisms. An evolutionary reality*. Berlin: Springer.

Novikoff, A. B. (1945). The concept of integrative levels and biology. *Science*, *101*(2618), 209–215.

Rohrmann, G. F. (1978). The origin, structure, and nutritional importance of the comb in two species of Macrotermitinae (Insecta, Isoptera). *Pedobiologia*, *18*, 89–98.

Rouland-Lefevre, C. (2000). Symbiosis with fungi. In T. Abe, D. E. Bignell, & M. Higashi (Eds.), *Termites: evolution, sociality, symbioses, ecology* (pp. 289–306). Dordrecht: Kluwer Academic.

Turner, J. S. (1994). Ventilation and thermal constancy of a colony of a southern African termite (*Odontotermes transvaalensis*: Macrotermitinae). *Journal of Arid Environments*, *28*, 231–248.

Turner, J. S. (2001). On the mound of *Macrotermes michaelseni* as an organ of respiratory gas exchange. *Physiological and Biochemical Zoology*, *74*(6), 798–822.

Turner, J. S. (2002). A superorganism's fuzzy boundary. *Natural History*, *111*(6), 62–67.

Turner, J. S. (2005). Extended physiology of an insect-built structure. *American Entomologist*, *51*(1), 36–38.

Turner, J. S. (2009a). Cognitive trap demo. Available at http://www.youtube.com/watch?v=8Q8N4vRMgXM.

Turner, J. S. (2009b). A swarm cognitive trap. *Macrotermes michaelseni*. Available at http://www.youtube.com/watch?v=WJCvsHJMWSM.

Turner, J. S. (2009c). Termite drinkers. Available at http://www.youtube.com/watch?v=7AOkb0epOgk.

Turner, J. S., & Soar, R. C. (2008). Beyond biomimicry: What termites can tell us about realizing the living building. In I. Wallis, L. Bilan, M. Smith, & A. S. Kazi (Eds.), *Industrialised, integrated, intelligent sustainable construction* (pp. 233–248). London, I3CON BSRIA.

van der Westhuizen, G. C. A., & Eicker, A. (1990). Species of *Termitomyces* occurring in South Africa. *Mycological Research*, *94*(7), 923–937.

Weir, J. S. (1973). Air flow, evaporation and mineral accumulation in mounds of *Macrotermes subhyalinus*. *Journal of Animal Ecology*, *42*, 509–520.

Wheeler, W. M. (1911). The ant colony as an organism. *Journal of Morphology*, *22*, 302–325.

Wilson, E. O. (1971). *The insect societies*. Cambridge: Belknap/Harvard University Press.

Wood, T. G., & Thomas, R. J. (1989). The mutualistic association between Macrotermitinae and *Termitomyces*. In N. Wilding, N. M. Collins, P. M. Hammond, & J. F. Webber (Eds.), *Insect-fungus interactions* (pp. 69–92). London: Academic Press.