Investigations into the building behaviour of a minor celebrity insect.

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ABSTRACT

People have long been fascinated with the striking, precisely aligned "magnetic" mounds built by termites of the genus *Amitermes* in northern Australia. Although the first written accounts that attempted to explain this alignment date to the late 19th century, it wasn't until Gordon Grigg rotated mounds and systematically measured their orientations in the 1970s that any substantial research was carried out to test these speculations. The ideas Grigg developed about the advantages offered by this remarkable architecture proved insightful and have shaped the subsequent thinking on the physiological effect of these mounds. This article reviews the concepts and research that have developed around this small but fascinating area of investigation.

Key words: termitaria, *Amitermes*, behaviour, orientation

Introduction

The north Australian termite *Amitermes meridionalis* is nothing to write home about: it is an average sized termite in its various castes; the soldiers appear to be rather timid when the mounds are broached and, being a grass-eater, it is not a fearsome destroyer of houses. The mounds that this termite species builds, however, are "probably the most famous structures built by termites" to quote an early leading authority on social insects (Emerson 1937). They look like enormous tombstones – with their long axes aligned north-south, and they can reach around 5m in height but most are around 1.5 – 3m tall. They occur in populations that can exceed 100 mounds and are always found in depressions or ill-drained flats south and west of Darwin that are water-logged from December to around May, but free of water from around June to November (Fig. 1). The outer parts of the mounds appear to be used for storage of the grass material the termites feed upon.

Similar meridional mounds are built by *Amitermes laurensis* in seasonally-flooded habitats further to the west, in Arnhem Land and Cape York Peninsula and by an undescribed *Amitermes* species in similar habitats south of Darwin (Ozeki *et al* 2007). Such meridional termite mounds are found nowhere else in the world.

In contrast to their makers then, these mounds certainly are something to write home about, and they have become minor celebrities featuring in numerous newspaper and magazine articles, television documentaries and even advertising campaigns (Fig. 2). These celebrities have also inspired wonder in many observers and have prompted a number of questions. Why do these termites construct such remarkably shaped mounds? What's more, why do these tiny, eyeless insects align such massive constructions to the

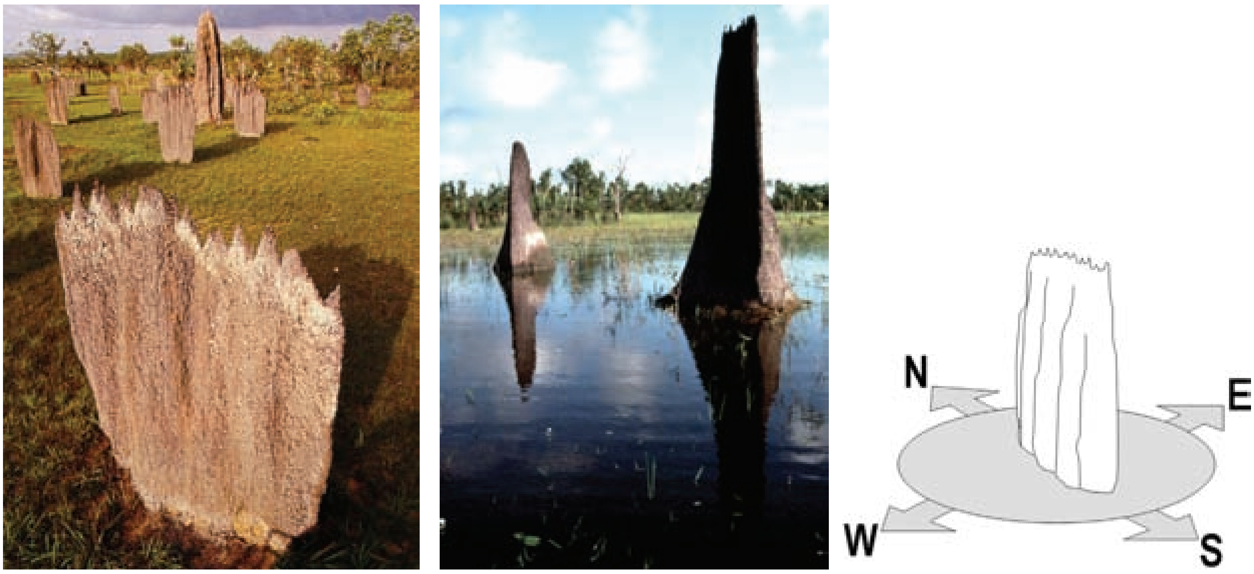

Figure 1. *A. meridionalis* mounds in dry conditions (left) and seasonally-flooded conditons (centre). The orientation is shown at right.

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meridian, a feat most people would struggle to achieve without using a compass? This story is about those, including Gordon Grigg and myself, who sought to answer these questions by scientific investigation.

Figure 2. A billboard advertising a milk drink on the side of a truck presumably refers to the way *A. meridionalis* termite mounds can save the lost traveller. This advertising campaign also played on the Northern Territory identity of the mounds.

The Early Observers

Indigenous people have long known of these mounds, but one of the first to speculate on their shape and orientation in western scientific terms was Robert Logan Jack, who held the position of Queensland Geologist and came across *A. laurensis* mounds in Cape York Peninsula during one of his many exploratory journeys of the late 19th century. Some mounds were so high he was "unable to touch the top with a riding whip while standing in the stirrups". He noted that in the wet season, these termites were engaged in mound building activity, and that their new work was quite fragile and looked susceptible to wind damage. Jack speculated that thin, flat mounds were aligned north-south to create east and west faces, exposing the new building work to intense rays of the sun for much of the day, and thereby allowing it to dry quickly despite the humid conditions (Jack 1897).

In 1910-11 the Swedish zoologist Eric Mjöberg led a Swedish scientific expedition to north-western Australia where he saw *A. meridionalis* mounds and a couple of years later he led an expedition to north Queensland where he was the first to taxonomically describe *A. laurensis*. He speculated that meridional mounds were aligned so as to shelter them from the prevailing winds (cited in Hill 1942).

Shortly after Mjöberg's trip, in 1912, Gerald Hill was appointed Government Entomologist in Darwin, a position he held until 1917. Unlike Jack and Mjoberg, Hill was able to visit meridional mounds repeatedly and he developed a particular interest in termites (Gay 1954). By the end of his career in the early 1940s he was working for CSIR and was Australia's leading authority on termites – his book *Termites (Isoptera) from the Australian Region* published in 1942 was the first comprehensive survey of termites in Australia. It was in that book that he outlined his explanation for the orientation of meridional mounds. He had observed that many tropical termite species, including *A.meridonalis*, appeared to move about their nests to seek out suitable temperatures – going to the base of the mound or underground in the heat of the day and seeking out the sunlit parts of the mound in the cool of the morning and evening. The meridional orientation should be particularly good at allowing termites to minimize temperature variation, as it offers them large areas of the mound that are heated during the cooler times of day (the east and west faces), while presenting only a thin aspect to the heat of the noonday sun (Hill 1942).

Hill also cast doubt on the earlier speculations. He pointed out it was unlikely that the rapid drying of new work in the wet season was the reason for the orientation as repairs and new work were effected at all times of year. (I have also observed that new work appears to dry rapidly on these mounds even in areas that are only obliquely illuminated by sunlight.) Hill also doubted that shelter from prevailing winds was an explanation as most gales were from the south-east – not directly from the north or south (Hill 1942).

However, why don't the other termite species that Hill claimed moved about their nests to minimize heat variation, also build meridional mounds? This was clarified by one of Hill's successors at CSIRO Francis Gay, who along with John Calaby, pointed out that many termites do not need mounds that were oriented to minimize temperature variation as they could simply move to underground galleries when necessary, an option that was not possible for termites in seasonally-flooded habitats. (Gay and Calaby 1970).

One further thought-provoking explanation for the orientation of the mounds was offered by the naturalist Vincent Serventy who postulated that the mounds were aligned to enhance ventilation within as they would often have one sunlit face at a high temperature while the other shaded face was cooler, and the resulting thermal gradients would drive air through the mound (Serventy 1967).

Testing the ideas

Gordon Grigg enters this story in the early 1970s when he was building a reputation as one of Australia's foremost ecological physiologists. While working on crocodile physiology in Arnhem Land in the Northern Territory, he noticed the meridional mounds of *A. laurensis* in the riverine flats west of Maningrida. Gordon decided to test the ideas of Hill, Gay and Calaby on the thermal significance of meridional orientation by rotating a mound by 90° so its long axis was aligned east-west. If a meridional orientation offered thermal advantages to the termites, then presumably such advantages would be destroyed by moving the mound to an opposite alignment.

Temperatures at points on the surface and inside of the mound were measured for three days in the north-south position and then for three days when rotated east-west. Grigg found that the core temperatures in the north-south mound, hovered around 34°C during the middle of the day. In the east-west orientation, however, the core temperatures rose to over 40°C creating significant thermal stress for the termites, thus supporting the ideas of Hill, Gay and Calaby as shown in Fig. 3 (Grigg 1973).

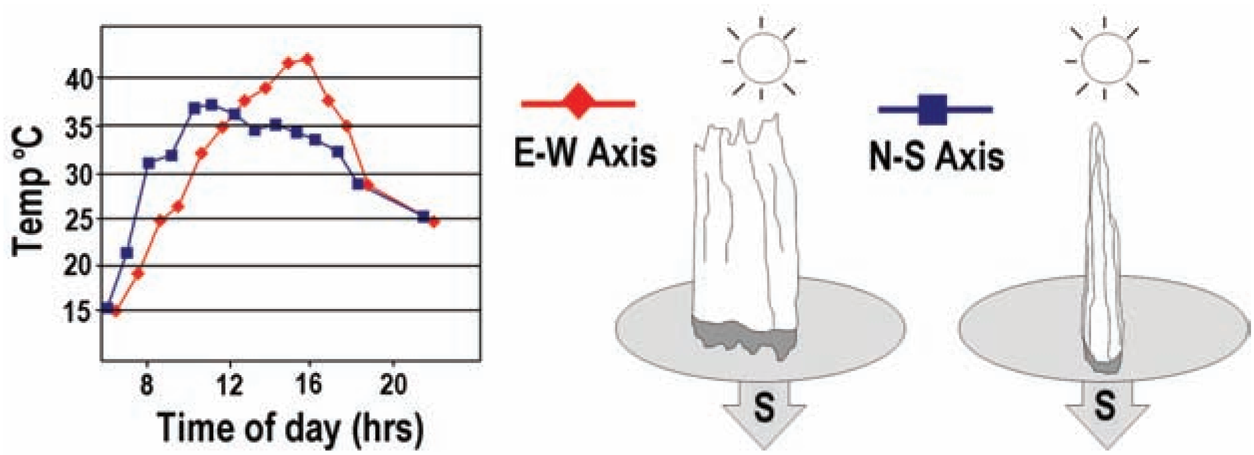

Figure 3. The effect of a 90° rotation on the core temperature, averaged over 3 days in both orientations, of an *A.Laurensis* mound in the north Australian dry season (modified from Grigg 1973).

Importantly Grigg then pointed out that while the meridional orientation of a wedge-shaped mound clearly aided thermoregulation, it was unlikely that the wedge shape *per se* was an adaptation for thermoregulation. Thermo-stable termite mounds tend to have dome or bulbous shapes with a low surface area: mass ratio such as the mounds built by *Bellicositermes natalensis* in Africa (Lüscher 1961). The thin, elongated meridional mounds, on the other hand, tend to have high surface area: mass ratios making them inherently thermally unstable and so require the north-south orientation to improve thermoregulation. Returning to Serventy's suggestion, it may be that the wedge-shape rather than orientation is an adaptation to enhance gas exchange by diffusion through the large walls, particularly in the wet season when dampness may decrease the porosity of the walls (Grigg 1973).

Another important factor was revealed by the experiment though not discussed in Grigg's paper. The experiment was conducted in June 1972 and at this latitude and time of year, the early-mid dry season, the sun moves in an arc tilted significantly north of the zenith. Consequently the north face of the east-west aligned mound had significant exposure to the northern sun for the whole day, including the intense irradiance from the midday sun and this would have produced the high core temperatures. It is highly unlikely that a similar change in core temperature would be produced by mound rotation in the wet season as clear days are less common and even then, as the sun would arc east to west close to the zenith, the vertical sides of an east-west mound would not receive strong irradiation. Indeed, simulations of the solar radiation on a vertical plate at that latitude show that it is mainly during the dry season that variation in orientation of the mound produces significant changes in solar radiation on the faces of the mound.

A testable hypothesis for mound orientation

I was a student of Gordon Grigg's in the late 1980s and I followed the basic blueprint that Gordon had already laid out for the study of these termites. Having a background in physics I was interested in how the orientation of these mounds may be interacting with the sun – rather than looking at other aspects of the mound shape.

I was also interested in the variation of orientation within and between populations of meridional mounds – another area of study opened up by Gordon Grigg. In the mid 70s he and Tony Underwood had measured and analysed the shape and orientation of a number of separate populations of *A.laurensis* mounds, some of which were in a more shaded habitat and found that the mean mound orientation did vary significantly by a few degrees between populations, but that this variation was not obviously related to the shadiness of the habitats (Grigg and Underwood 1977). A similar study of mean mound orientation of a range of termite mounds was carried out by Alister Spain and others and their survey included *A. laurensis* meridional mound populations in Cape York Peninsula. Again, no obvious correlation between the variation in mean orientation of these meridional mounds and environmental factors was observed (Spain *et al* 1983).

When I measured the mean orientation of a large number of *A. meridionalis* populations south of Darwin, however, there did appear to be variation related to environmental gradients: populations nearer the coast tended to have mean orientations further to the west and those in more shaded habitats tended to have more variable orientations (Jacklyn 1991). If this variation was an adaptive response to different environmental conditions, then it raised the possibility of developing a testable hypothesis on orientation. Gordon's mound rotation experiment had shown that orientation had a major influence on mound temperature, however, we could not confirm that the termites were benefiting from the meridional orientation: we did not know much about the internal response of the termite colony to temperature and termites did not construct east-west mounds that were then abandoned. The variation in orientation of *A. merdionalis* mounds suggested that there may be a favourable thermal property of the mounds that was sensitive to much smaller changes in mound orientation, such that mounds constructed more than 10 or 20° away from the optimum orientation in a given location were penalized. If we could find out what thermal properties were sensitive to small changes in orientation we could test out ideas of their biological significance by seeing if we could then predict how mound orientation should vary with environmental conditions.

I repeated Gordon's mound rotation experiment but with *A. meridonalis* mounds and rotating the mounds through only 20° to reflect the observed variation in orientation. Whereas Gordon rotated the rather thin *A.laurensis* mound by cutting through the base with a cross-cut saw and then turning the upper part of the mound, I was faced with *A. meridionalis* mounds that were much thicker at the base and, after destroying a cross-cut saw, rotation of these mounds was achieved by nudging them with 4WD vehicle which loosened the whole structure from the floodplain – the mounds were then slowly turned to the desired orientation using a rocking motion. The rotation was conducted in the dry season when the solar geometry would ensure small changes in orientation would produce significant changes in irradiance on the mounds. The results showed that these small changes in orientation did alter a thermal property of the mounds that had potential biological significance: the eastern face temperature. Normally-oriented mounds had a stable temperature plateau on their eastern face for much of the day from late morning, yet rotating the mound 20°W caused a significant rise in the temperature plateau on this face during the day, and rotating the mounds 20°E caused a corresponding drop in this temperature plateau (Fig 4).

Having relatively stable temperatures around 30°C over a large area of the mound where food material is stored could have advantages for the termites. Furthermore, the behaviour of the termites suggested they were indeed aligning mounds to create such a plateau: mounds in locations where wind or shade reduce the heating of the eastern face tend to be oriented further to west – and heat transfer analysis showed that the degree of this shift to the west is about what would be needed to catch enough extra solar radiation on the eastern face in the dry season to counteract the cooling (Jacklyn 1992). This, at least, was an explanation for the orientation of *A. meridionalis* mounds that could be further tested to determine if the orientation of unsurveyed populations of these mounds also varied with wind and shade conditions so as to maintain the temperature plateau.

Some Reflections

Even if this pattern in the orientation of *A. meridonalis* mounds is confirmed, it is still far from clear precisely what benefits accrue to the termite colony by such an orientation, nor is it apparent that the variation in the orientation of *A.laurensis* mounds can be explained similarly. Genetic drift may be more significant in influencing the orientation

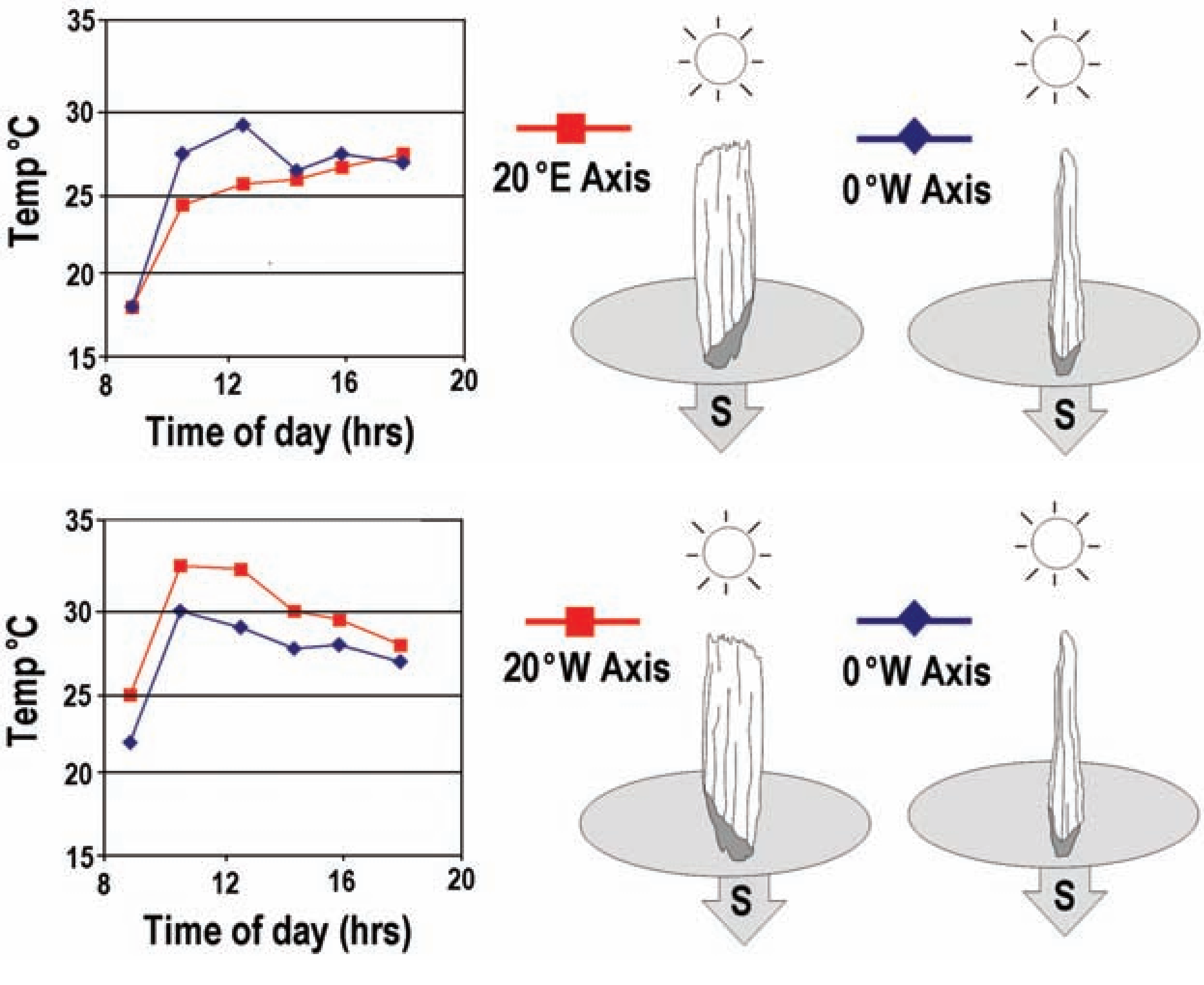

Figure 4. The effect of small changes (20°E on top, 20°W on bottom) in orientation of *A. meridionalis* mounds in the dry season on the temperature of the eastern face. Such changes were consistent across all 21 mounds involved in the experiment.

of *A.laurensis* mounds – and despite the findings above, genetic factors may also strongly influence the variation in *A. meridonalis* mounds. And as Gordon pointed out, even if you can explain orientation this does not necessarily explain the adaptive significant of the overall mound shape. This question is now being addressed by Judith Korb and Anna Schmidt from Regensberg University in Germany who are investigating the interaction of mound shape and habitat shading on mound temperature and gas concentrations in *A. meridionalis*.

It is interesting to note that these mounds attract the interest of researchers partly because of their beguilingly simple shape and starkly uniform alignment – yet this behaviour remains remarkably difficult to explain convincingly. I suspect that much of this difficulty stems from a lack of knowledge of the basic biology of these termite colonies. Meridional mounds could conceivably have significant roles in functions of the enclosed termite colony including reproduction, feeding and food storage, microclimate regulation, waste disposal and population regulation, therefore these factors could influence the internal and external shape and orientation of the mound. Yet we know little about most of these aspects of colonies of *A. meridionalis* or *A. laurensis*. What role do the faces of the mounds have? How important is the mound core? Are separate mounds connected? By contrast when we come across a little-studied vertebrate we can draw on a vast store of prior knowledge on the broad functions of organs and parts of the body.

If explaining the shape of these mounds is so difficult, why bother? The first point to make here is that architects can profit from understanding how termite colonies are able to establish stable microclimates in mounds. The architect Mick Pearce has designed several buildings that use elements of the air-conditioning system employed by the fungus-gardening termites of the sub-family Macrotermitinae. By building elaborate ventilation passages and evaporative cooling into their mounds these remarkable insects can maintain an internal temperature that only fluctuates by a degree or two despite fluctuations in the outside air temperature of tens of degrees – and the buildings use a similar system to achieve very energy efficient air-conditioning (Turner and Soar 2008). Australia's meridional mound-builders, however, do not construct similar ventilation systems and have established a much coarser degree of temperature control through orientation of the mound.

Nevertheless can human architects learn something from these meridional mounds? Orienting buildings to expose them to particular solar radiation patterns has long been used by some architects to help control internal temperature and ventilation – however, meridional elongation of buildings for thermal benefit appears uncommon, indeed residential buildings in warm climates are sometimes elongated along an east-west axis so that the sun tracks along the roof during the day leaving most of the windows and walls more shaded (Earle and Jaffe 1997). Generally, orientation of buildings would appear to be influenced by the available block shape, and factors other than solar angles and this is probably because the internal environments of small and thin meridonal termite mounds are much more sensitive to orientation than are the insides of our buildings – the surface area: volume ratios of meridonal termite mounds are hundreds of times larger than those of buildings. It was Gordon Grigg who first pointed out that the merdional orientation of these mounds could be seen as a solution to a specific problem faced by these termite colonies - the thermal instability of a small, thin flat plate under a tropical sun. So one lesson for architects may be that as solutions to architectural problems in nature usually arise through natural selection operating in response to specific environments, such solutions may not work when applied more generally.

There is another benefit to consider: one reason these meridional termites have become minor celebrities in this country is because they are seen as distinctively Australian and it can be argued that we should have a good understanding of the biology of our celebrated, distinctively Australian fauna and flora so they can be better managed and protected. Meridional termite mounds do face potential threats – in Cape York Peninsula, for example, the habitats of many meridional *A. laurensis* mounds are undergoing significant change through the thickening up of *Melaleuca* and other species (Garnett and Crowley 1995, p.22). This vegetation change is likely to be affecting food availability and shade conditions.

Finally one can't help wondering where the state of our understanding of these termites would be were it not for Gordon Grigg. Advancing the understanding of meridional termite mounds was not exactly a research priority in 1972, but thanks to Gordon's curiosity and a few short but insightful studies he was able to frame the key research questions to be addressed.

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