Solar Engineering for the Blind: "Magnetic" Termite Mounds of the Top End

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Abstract

The termites *Amitermes meridionalis* and *A. laurensis* construct meridional mounds across northern Australia which vary geographically in mean orientation from 11° E to 15° W in a manner that suggests such variation is an adaptive response to local environmental conditions. Theoretical modelling of solar irradiance, mound rotation experiments and analysis of weather conditions show that maintenance of an eastern face temperature during the dry season explains the variation in mound orientation. This is affected by wind speed and shading conditions. Further study of the spatial and temporal distribution of mound orientations, together with experiments on mound growth in magnetic fields, indicates that the mounds are constructed along inherited magnetic cues and that natural selection matches mean mound orientations to environmental conditions.

Introduction

The most famous architects of the Top End region of the Northern Territory are a few millimeters long and blind. The spectacular tombstone-shaped "magnetic ant-hills" in this region are constructed by the worker caste of the termite *Amitermes meridionalis* (Froggatt). Termites are social insects, related to cockroaches, not ants. Their diet is based on cellulose. Colonies of *A. meridionalis* collect plant litter using subterranean galleries radiating from the mound. This material is then stored in the outer galleries of the mound and used to feed the colony. The mounds are constructed on the edges of seasonally flooded alluvial flats extending from Koolpinya in the north to the Daly River in the south. Mature mounds are large flat plates, around 2 m high, which taper from a massive base to a turreted ridge that is oriented along a north-south axis (Cover Plate). Thus each mound is approximately aligned with a meridian of longitude, giving the specific name *meridionalis*.

The mounds are remarkable in a number of ways. First, although they may be a familiar feature of the bush to Top End residents, in the context of termite mounds world-wide, they are spectacular oddities. Termite mounds are found throughout the tropics and are generally conical, cylindrical or dome-shaped. Clustered, plate-shaped mounds aligned in the same direction, occur only in northern Australia. Such meridional mounds are built by at least three termite species in northern Australia: *A. meridionalis*, *A laurensis* (Mjoberg) and *A. vitiosus* (Hill). The last species does not commonly build meridional mounds and was not included in this study.

The precise shape of these mounds is a key to explaining their function. Because the mounds are always constructed in seasonally flooded ares, their shape is probably adapted to these habitats. Various explanations for the adaptive value of meridional mounds have been advanced (Jacklyn 1991), but none of them satisfactorily explain the geographic variation in mound orientation described below.

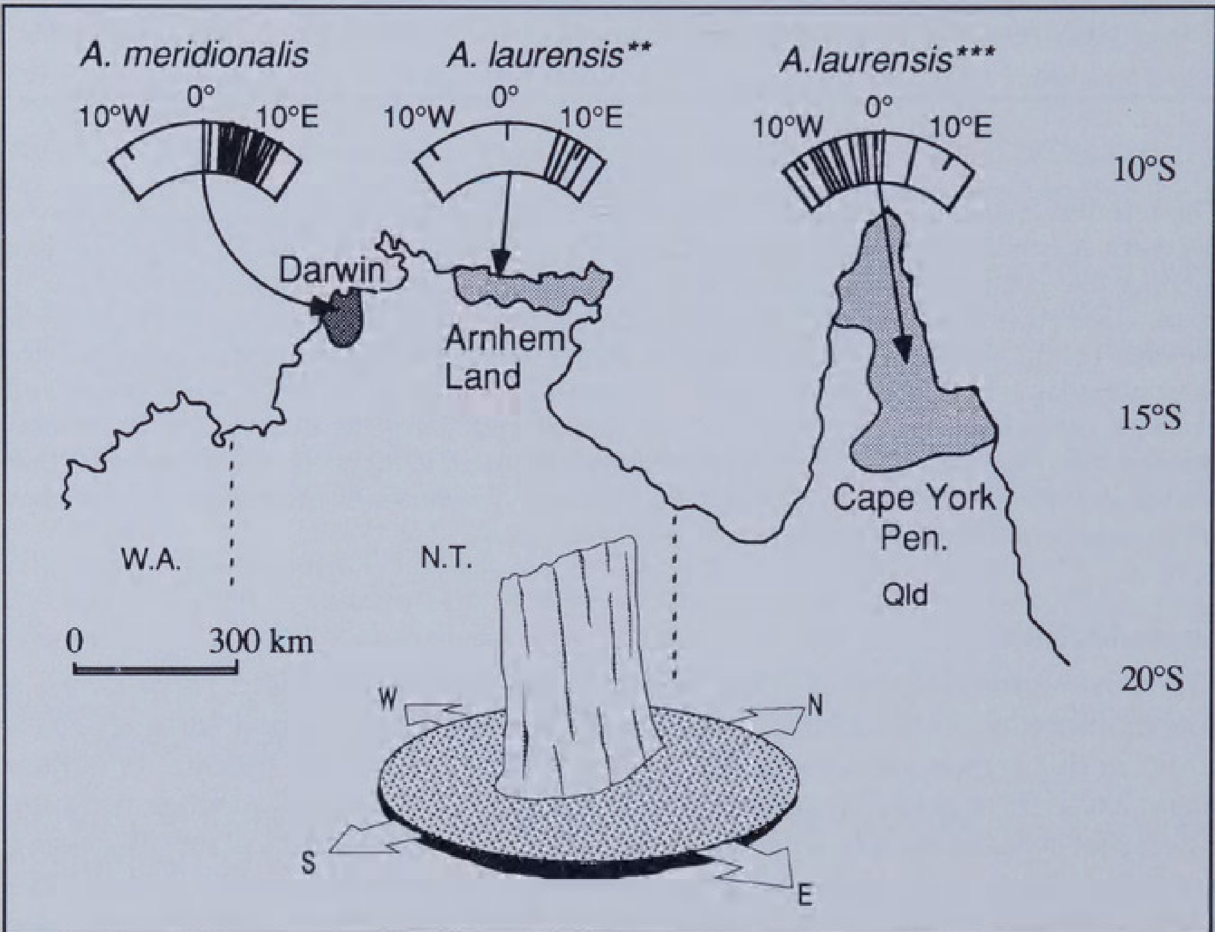

FIGURE 1 The distribution of meridional mounds and the variation in mean mound orientation of 47 *A. meridionalis* sites near Darwin, 4 *A. laurensis* sites in Arnhem Land and 17 *A. laurensis* sites in Cape York Peninsula. Each angular line represents the mean geographic orientation of 20 - 50 mounds (note: several sites have the same mean orientation). **, Grigg & Underwood (1977); ***, 13 sites from A. Spain (unpubl. data); all other sites surveyed by the author.

Variation in Mound Orientation: a model

Measurement of the orientation of a large number of *A. meridionalis* mounds makes it clear that these mounds are not like compass needles, all oriented to magnetic north, nor are they strictly meridional, all oriented to geographic north. Rather, mound populations vary in mean orientation from 0° (geographic north) near the coast at Mandorah, to 10° E (geographic) in the south of Litchfield Park. Similarly, populations of 'meridional' *A. laurensis* mounds in Cape York Peninsula and

Arnhem Land vary in mean orientation from 10° E in Arnhem Land to 15°W in Cape York (Fig. 1; Grigg & Underwood 1977; Duelli & Duelli-Klein 1978; Spain *et al.* 1983; Jacklyn 1991). This variation follows the broad environmental gradient between inland and coastal regions around Darwin, and between the Top End and Cape York Peninsula across northern Australia.

A possible explanation for this pattern is that the mounds are conserving some physical property that is important for termite survival, and is dependent on both the mound orientation and environmental conditions. Thus, maintaining such a property is a matter of adjusting mound orientation to suit local environmental conditions, and, as these conditions change, the optimum mound orientation also changes. But what mound property could be sensitive to such small changes in mound orientation as well as being sensitive to environmental conditions? One way of finding out is to rotate meridional mounds through the small differences in orientation seen between populations and see what physical properties are consistently changed. When this is done an intriguing phenomenon emerges: the mounds seem to be oriented so that they maintain a temperature plateau on the eastern face of the mound during dry-season days. In other words, unlike almost any other organism in the world, they create a thermostable surface on one side of a large plate.

This temperature plateau is sensitive to two factors:

The orientation of the mound and the time of year.
During the dry season when the sun describes an arc across the northern sky, the pattern of solar irradiance on each face is critically dependent on mound orientation. Mounds oriented more to the *northwest* receive more radiation on their *eastern* faces: this face is heated above air temperature by the middle of the day, and tends to cool down in the afternoon. Mounds oriented more to the *northeast*, on the other hand, receive more radiation on their *western* faces, and the cooler *eastern* face tends to warm in the afternoon (Fig. 2).

Wind and shade conditions
South-easterly trade winds blowing on the eastern face of the mound during the dry season will lower face temperatures in the morning when air temperatures are low. Thus, for mounds to maintain optimum eastern face temperatures in areas exposed to the dry season winds, they will have to be oriented more to the west than more sheltered mounds, so that the east face collects more radiant heat to offset the wind effect.

Similar arguments show that mounds in shaded habitats with shadows (from either trees or clouds) passing across their eastern faces should also be oriented more to the west. Because habitats shaded by vegetation contain a range of shade micro-habitats from unshaded to completely shaded, one would expect a random sample of mounds from such habitats to have a greater variance in orientations than a sample of mounds from nearby open habitats. According to this model of mound orientation, the observed variation in mean mound orientation across northern

Australia is caused by the geographical variation in long-term wind and shade conditions.

Testing the Model

If the above model is correct, i.e. the mounds are conserving a dry season eastern face temperature plateau, it should be possible to predict the expected variation in mean orientation of meridional mounds across northern Australia by referring to long-term wind speed and cloud cover records. Sure enough, these predictions match the observed variation in mound orientation: the mounds on the coast near Mandorah are a dew degrees west of mounds in Litchfield Park as one would expect given the higher coastal winds during the dry season; mounds in shaded habitats are more variable in orientation than mounds in nearby open habitats; the *A. laurensis* mounds in Cape York Peninsula are oriented well to the west of mounds in the Top End (Fig. 1) because they experience the high winds and cloud cover associated with the passage of easterly trade winds sweeping in off the Pacific Ocean during the dry season (by the time these winds reach the Northern Territory they are weaker and drier).

How 'Magnetic' Termites Construct their Mounds

If the feat of small, blind insects constructing a massive plate a thousand times higher than themselves is enough to boggle the mind, then the ability of the same insects to orient this plate so that it matches long-term dry season wind speed and cloud cover conditions is quite incredible. This incredulity is strengthened by the observation that most mound construction occurs during the wet season - the time of year when these climatic cues are absent.

Not unexpectedly perhaps, observation of mound growth and the distribution of mound orientation suggest that mounds are constructed along a fixed axis. That variation in mound orientation within populations decreases with age further suggests that mound orientation is matched in environmental conditions by natural selection: mounds built along genetically fixed axes appropriate to the local climatic conditions grow to maturity and make a contribution to the next generation of mounds; mounds built along inappropriate axes do not reach maturity and the genes for that axis are weeded out of the population gene pool. This orientation mechanism makes the mounds vulnerable to rapid changes in climate - cause for concern, given predictions for the effects of increasing concentrations of atmospheric greenhouse gases on the earth's climate.

In the light of these investigations, the name 'magnetic' mound may seem inappropriate, but when one considers the ways in which a genetically inherited directional cue might be used by termites, the use of magnetic cues seems an obvious possibility. Therefore, I investigated the effect of changes in the direction of the surrounding magnetic field on mound growth. Although these experiments could only be carried out on mound repair (the axial extension of the mound that occurs in normal growth takes many years), the internal structure of the repaired part of the mound was aligned with the magnetic field in a manner consistent with the use of magnetic declination to orient the mound. This is not to say that the termites align the mound with magnetic north, but that they align it along an inherited magnetic axis with a bearing that is likely to be appropriate to the long-term wind speed and shading conditions of the habitat (assuming the colony was founded by alates from a nearby mature mound).

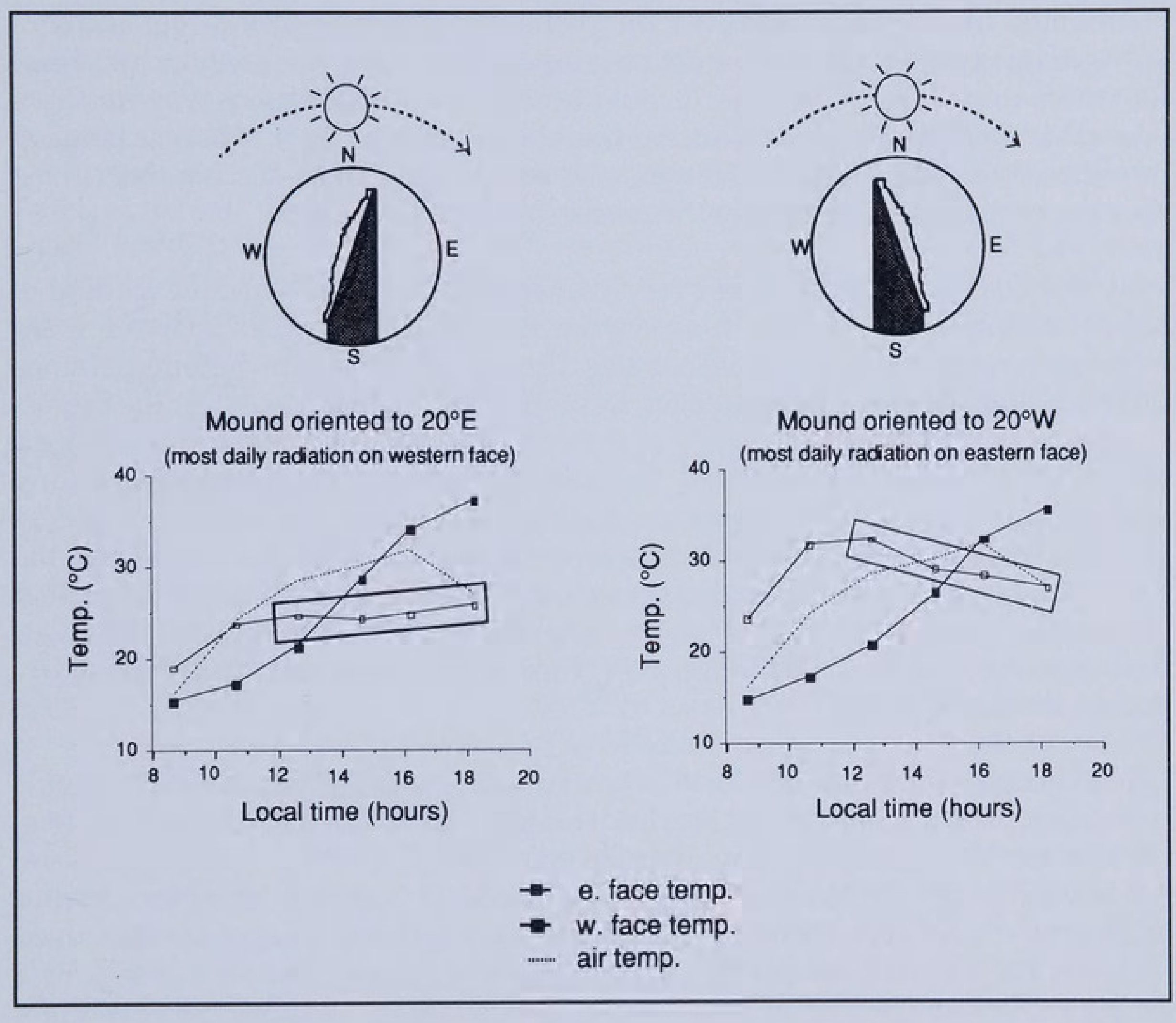

FIGURE 2 The effect of mound orientation on eastern face cooling (boxed areas). Plan view of mounds shown above each temperature graph.

This suggestion raises as many questions as it answers. How do termites detect magnetic cues? (Other insects have been found to have magnetic receptors: Becker 1963; Becker & Speck 1964; Martin & Lindauer 1977). What is involved in inheriting a colony trait like mound orientation, which is the product of the combined behaviours of many termites, each with their own slightly different genetics? (see Dawkins 1982, for an interesting discussion on this point, featuring none other than 'magnetic' termite mounds). What happens when the magnetic field changes direction over time? The earth's magnetic field has its origin in the electrically conductive molten iron that surrounds the earth's core; consequently it is not fixed in direction but varies slowly over time. This secular variation has been tracked ever since sailors first used compasses, and in most parts of the world, the direction of the magnetic field changes by a few degrees every century. This should pose problems for long-lived termite colonies (old colonies may live for over 100 years) which depend on the magnetic field to provide a directional cue that is sufficiently stable to be a useful guide to a precise geographic orientation over many generations of mounds. Interestingly, however, the geomagnetic field direction over northern Australia is unusually stable, hardly varying at all over the last few hundred years for which records are available. It could be that one of the reasons why northern Australia (and possibly New Guinea) has at least three or four different kinds of meridional termite mounds (whereas the rest of the tropics have none), is the stability of the magnetic field in the northern Australian region.

Why should these termites have evolved such an awkwardly sensitive method of temperature control? The key to seeing the advantages of such an adaptation lies in the nature of seasonally flooded habitats. During the wet season these depressions offer advantages and disadvantages to plant litter feeding termites: the water-logging produces abundant stands of the spear grass *Sorghum intrans* which are a source of nutrition for termites; the same water-logging also destroys any underground refuges of the termites, and they are trapped in the mound above ground. During the dry season these areas are moist enough (perhaps through the dew-fall associated with nocturnal cool air drainage) to support plenty of annual grasses that provide more food for the termites; however, the vagaries of cool air drainage also give these habitats great variation in air temperature and humidity during the dry season.

Other species of termites cope with a variable environment by building mounds with a complex internal architecture that creates a stable internal environment (e.g. see Luscher 1961), or by moving underground (Bouillon 1970). These options are not available to *Amitermes* in seasonally flooded habitats: complex mound architecture is not seen in this genus and any underground refuges are destroyed by water-logging that can persist into the early dry season. One way of making a simple mound shape thermo-stable is to make it massive. Another, more efficient solution is to construct it as a surface, the thermostability of which is determined by its orientation to the sun and the wind and shading conditions. The more flat and elongated the mound is, the more living space is incorporated into the thermostable regions of the mound.

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