



Thermal regulatory mechanisms of termites from two different savannah ecosystems



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ARTICLE INFO

Keywords:

Adaptation
Sahel
Sudan
Shade
Open
Mound architecture
Temperature regulation

ABSTRACT

Termites are known for their abilities to regulate the conditions within their nests through the mounds that they build or the location of the built mound which assist in keeping the internal temperature within the requirement of the colony. These mechanisms to regulate vary between species, with some species adapting passive behaviours such as nest site selection and nest structures that permit passive heating or cooling. Here we studied seven species of mound building termites from five genera in two different savannah (Sahel and Sudan) and determined some of their passive thermal control strategies. Seven species of termites; *Amitermes* sp., *Cubitermes oculatus*, *Macrotermes bellicosus*, *M. subhyalinus*, *Odontotermes* sp., *Trinervitermes* sp. A and *Trinervitermes* sp. B were identified from the two savannah. We found no significant difference in internal mound temperatures between the species. In both savannah types most of the termites built their nest under the shade. We discuss the adaptive implications of building mounds under the shades as seen in species of *M. bellicosus*, *M. subhyalinus* and *Odontotermes* sp. Or those building mounds with unique shapes as seen in *C. oculatus* with mushroom shaped mounds for their role in thermal regulation within the nest and how this represents a response to environmental conditions.

1. Introduction

Temperature is one of the important abiotic factors that determines the geographic distributions of termite species (Kofoid, 1934). Tropical termites are physiologically adapted to a narrow range of climatic conditions, and as a result may be particularly affected by changes in ambient temperatures (Dahlsjö et al., 2015; Korb and Linsenmair, 2000). Living in large colonies and nesting in thermally inert materials (soil or wood), buffers these environmental fluctuations (Korb and Linsenmair, 2000). However, just buffering might not be sufficient, especially for fungus-growing termites which requires constant warm temperatures, high humidity and an efficient exchange of respiratory gases to culture the needed symbionts (Korb and Linsenmair, 1999). Hence the requirements by fungus-growing termites to build mounds adapted to these challenging demands. For instance, the African and South-East Asian large termite *Macrotermes bellicosus* constructs cathedral-shaped mounds with thin walls and many ridges in open savannahs which allows excess temperature to be expelled from the mound thus creating optimal temperature conditions. But in forests where temperatures are low, *M. bellicosus* constructs dome-shaped mounds with thick walls and a low surface complexity allowing for less exchange between the mound and the environment (Collins, 1979; Lüscher,

1956). In arid regions termite mounds are adapted to conserve water, while the famous north-south elongated magnetic termite mounds in Australia is an adaptation to seasonal flooding and temperature (Korb and Linsenmair, 1998b). Thus, as selective regimes differ between areas, termites adapt their mound architecture to suite these changes. Termites have become much more independent of the environmental conditions by building mounds, allowing them to control and regulate the conditions within their nest (Howse, 1970). Besides the benefit of being less exposed to the environment, the ability of nest homeostasis allows for the optimisation of local specific conditions, like high humidity for juvenile termites, which are susceptible to water loss or to maintain a fungus garden. Another advantage of building mounds is of course, that a mound keeps predators and parasites out (Jouquet et al., 2015).

Nest architecture is thus an expression of innate behaviour, modified by interactions with the environment (Noirot and Darlington, 2000). Termites can have different temperature tolerance limit as seen in *Coptotermes formosanus* which exhibit higher temperature tolerance and *Reticulitermes flavipes* which displays low tolerance limit to temperature (Sponsler and Appel, 1991). Ambient temperature influences the type of ventilation directly by determining the temperature patterns in and around the mound and indirectly by determining the mound's

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<https://doi.org/10.1016/j.jtherbio.2019.102418>

Received 13 June 2019; Received in revised form 27 August 2019; Accepted 11 September 2019

Available online 13 September 2019

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structure (Korb and Linsenmair, 2000a) and colony activity (Fuchikawa et al., 2012).

But not only nest structure regulates internal nest conditions, behavioural strategies are as well able to contribute to these regulation for example, evaporative cooling, or if water is scarce, abandoning section of the mound by retreating to cooler and more humid parts of the mound (Sunday et al., 2014). From a certain size of the colony heat generated by metabolic activity become a factor which has to be regulated that also allows colonies to be independent of environmental conditions (Sunday et al., 2014; Buckley et al., 2013; Klingner et al., 2005; Huey et al., 2003; Noirot and Darlington, 2000; Korb and Linsenmair, 2000).

Although it is known that termites use different means of thermoregulations that are either active or passive (Stein et al., 2014). With active temperature regulation referring to behaviours where individuals modify nest temperature through physical activities like evaporative cooling. Passive temperature regulation on the other hand includes mechanisms as nest site selection, nest structures that permit passive heating or cooling, or simple behaviour such as brood translocation to regions within a nest where temperatures are most favourable (Danks, 2002). It is also established that mounds show significant variation within an ecosystem (Woon et al., 2019; Erpenbach and Wittig, 2016; Noirot and Darlington, 2000; Korb and Linsenmair, 1998a), less is known about the comparison within a species but between different broader habitats and ecological zones.

Factors affecting the distribution of termite species are seasonal periodicity and rainfall thus making the savannahs an ideal habitats for termites (Davies et al., 2014; Pearce, 1997). The vegetation zones in Nigeria and the abundance of termites in different savannah makes Nigeria an ideal place to test our hypothesis on thermoregulation between habitats due to the diversity of termites and their ecologies as influenced by soil types, vegetation, land use and climate (Abe et al., 2009; Collins, 1981; Orhue et al., 2007). The vegetation zones in Nigeria correspond to different climatic regimes, which are delineated by edaphic conditions particularly drainage and biotic factors with the climate becoming drier as one travels inland from the coast (Ola-adams and Iyamabo, 2009). Major vegetation formations are the savannahs which forms four-fifths of the land area that consist of Guinea, Sudan, and Sahel savannah with the forests covering one-fifth of the land (Ola-adams and Iyamabo, 2009). We hypothesise that termites utilise plant cover to thermoregulate. Therefore, we predict that termites in warmer habitats are significantly more likely to build mounds in shaded habitats. Since mounds play a role in thermoregulation we also predicted that termites in warmer areas within habitats are more likely to build mounds with specific shapes (mushroom) associated with a reduced internal temperature.

2. Materials and methods

Study sites: The study was conducted in ten (10) localities: (five each from Sahel and Sudan savannah) (Fig. 1). The Sahel savannah has a mean annual rainfall of between 250 mm and 510 mm, and the dry season that last for 7–8 months whilst the Sudan savannah is characterised by mean annual rainfall of 510 mm–1140 mm, with the dry season that last for 5–7 months (Ola-adams and Iyamabo, 2009). The natural vegetation is characterised by open woodlands with scattered trees such as *Faidherbia albida*, *Parkia clappertoniana*, *Borassus* spp, *Euphorbia obtusifolia* and *Hyphaene thebaica* from Sahel savannah. Whilst Sudan savannah is characterised by medium sized trees such as *Parkia clappertoniana*, *Vitellaria paradoxa*, *Diospyros mespiliformis* and *Combretum* species.

2.1. Mound location and architecture

In each of ten sampling locations (Fig. 1) three quadrats of 50 m × 50 m that are accessible were made and sampled for the

presence of mound building termites and their mounds (Yusuf et al., 2014). From each of the set of quadrats mentioned above, three active mounds were selected, georeferenced using a handheld GPS *Garmin III* (Garmin, USA). A total of 270 (135 each from Sahel and Sudan savannah) active mounds were studied. Activity of the mounds were determined by measuring the carbon dioxide (CO₂) within the mound (data on request). Internal and external temperatures were also recorded, both CO₂ and temperatures were measured using an Omniport 30 multifunctional handheld meter (E + E Elektronik GmbH Austria). Visual recording of the shape of each mound was made using a Canon SX430 HDX 20.0 mega pixel optical 45× zoom plus 90× camera (Japan) and classified into four; cathedral, cone, dome and mushroom shapes. Depending on their locations, mounds were also grouped into the following two categories; in the shade or in the open.

2.2. Measurement of mounds internal and ambient temperatures

Both internal and ambient (2 m away from the mound) temperatures were measured using an Omniport 30 Multifunctional handheld meter (E + E Elektronik GmbH Austria). To measure internal nest temperatures, a hole of about 2 cm wide was drilled in to the wall of the mound using a customised made 50 cm long metal rod, this allows the sensor rod of the Omniport to be inserted into the mound and sealed tightly using sand particles. A lag time of 60 s was allowed prior to taken any reading in order to exclude interference from external air. Aside from the data measured in the field, long term (between 1982 and 2012) annual mean ambient temperature and rainfall data (Fig. 4) for the study area were obtained from an open source repository climate-data.org (climate-data.org) in order to compare changes in temperature and rainfall over time.

2.3. Termites' identification

In order to identify the termites, representative soldier castes were collected from each of the sampled mounds and stored in 70% ethanol. Whilst in the laboratory, termites were identified to species level where possible using morphometric keys that are based on characters like head shape, arrangements of notum, shape and colour of notum, number of antennal segments (Vivienne, 2002). *Cubitermes* and *Macrotermes* were identified to species level using keys by Ruelle (1970) and Korb (unpublished data). Whereas *Amitermes*, *Odontotermes* and *Trinervitermes* were only identified to the generic level and separated into species but not assigned names due to lack of established keys and taxonomic revisions for west African termites (Korb et al., 2019). A reference collection for the samples is lodge at the Department of Zoology and Entomology University of Pretoria South Africa.

2.4. Statistical analyses

We ran a Mann-Whitney's *U* test to evaluate the differences in the internal mound temperatures of the same species from the two savannah. Logistic regressions were performed to assess the impact of temperature on the likelihood that mounds will be built in the shade or in the open. While an independent-samples *t*-test was performed to compare the average ambient temperature and rainfall for the long term data (between 1982 and 2012), when the proportion was less than 5 fishers' exact test was used and alpha - level was set at 0.05.

3. Results

3.1. Termite species, shapes and location of mounds

A total of 270 mounds belonging to 5 genera and seven species of termites were monitored in the study area. The termite species found were; *Amitermes* sp. *Cubitermes oculatus*, *Macrotermes bellicosus*, *M. subhyalinus*, *Odontotermes* sp., *Trinervitermes* sp. A and *Trinervitermes* sp.

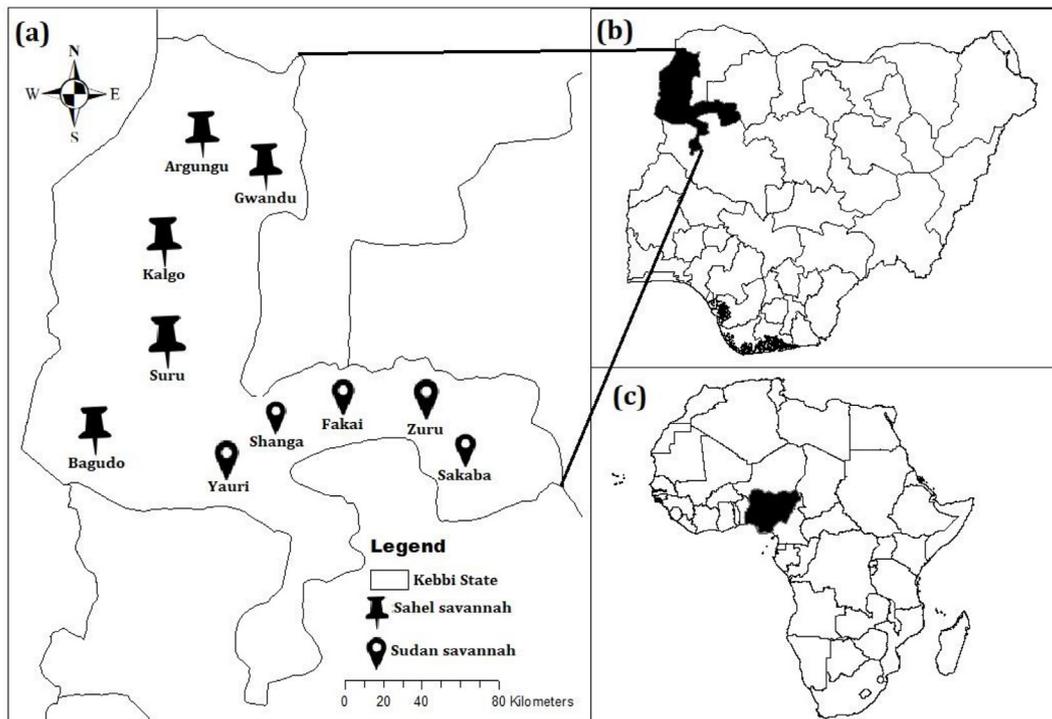


Fig. 1. (a) Map of Kebbi State and the sampling sites from Sahel (♣) and Sudan (📍) savannah within the State (b) Nigeria showing Kebbi State and (c) Map of Africa showing Nigeria.



Fig. 2. (a) Open cone shape mound of *Trinervitermes* sp. A (Height 22 cm) (b) Open mushroom shape mound of *Cubitermes oculatus* (Height 39 cm) (c) Open dome shape mound of *Macrotermes bellicosus* (Height 332 cm) (d) Shaded cathedral shape mound of *Macrotermes bellicosus* (Height 297 cm) (e) Shaded dome shape mound of *Trinervitermes* sp. A (Height 97 cm) (f) Shaded mushroom shape mound of *Cubitermes oculatus* (Height 20 cm).

B. Cone, mushroom, dome, and cathedral shape mounds (Fig. 2a, b and 2f, 2c and 2e, and 2d respectively) were observed in both Sahel and Sudan savannah. All nests belonging to *Amitermes* sp. were cone and dome shaped for Sahel and Sudan savannah respectively (Table 1). Most (82%) of *C. oculatus* mounds from the Sahel are mushroom shaped and those from Sudan savannah were all cone shaped. For *M. bellicosus* from Sahel most (80%) of their mounds were cathedral shaped, while in the Sudan they show no preference for cathedral or domed shaped mounds (Table 1). Dome shaped mounds were dominant features for *M. subhyalinus* with 93% and 89% for Sahel and Sudan respectively. Whilst

all mounds of *Odontotermes* sp. from Sahel were dome shaped with no preferences for both cathedral and dome shaped mounds in the Sudan. *Trinervitermes* sp. A showed preferences for cone shaped mounds in both Sahel and Sudan whilst *Trinervitermes* sp. B from the Sahel built mainly dome shaped mounds and cone shaped in Sudan savannah.

Majority (74%) of the termites mounds studied from the Sahel savannah were found in the shade (Fig. 3 and Table 2). Similarly, 53% of the mounds from the Sudan savannah were also built in the shade. Mounds in the open belonging to *Trinervitermes* sp. A, *C. oculatus* and *M. bellicosus* are shown in Fig. 2a, b and 2c, while shaded cathedral

Table 1
Percentage (%) of mound shapes found in Sahel and Sudan savannah.

Species (n = Sahel, Sudan)	Cathedral		Cone		Dome		Mushroom	
	Sahel	Sudan	Sahel	Sudan	Sahel	Sudan	Sahel	Sudan
<i>Amitermes</i> sp. (2,2)	-	-	-	100%	100%	-	-	-
<i>C. oculatus</i> (28,4)	-	-	7%	100%	11%	-	82%	-
<i>M. bellicosus</i> (20,10)	80%	50%	-	-	20%	50%	-	-
<i>M. subhyalinus</i> (74,46)	4%	7%	3%	4%	93%	89%	-	-
<i>Odontotermes</i> sp. (4,2)	-	50%	-	-	100%	50%	-	-
<i>Trinervitermes</i> sp. A (5,61)	-	-	80%	80%	20%	20%	-	-
<i>Trinervitermes</i> sp. B (2,10)	-	-	-	80%	100%	20%	-	-

n = sample size.

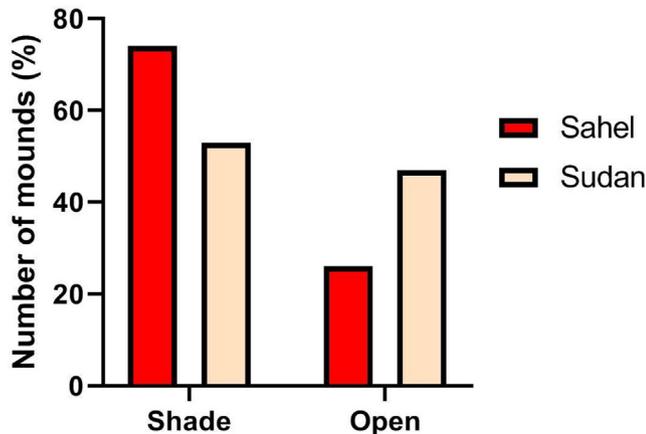


Fig. 3. Percentage (%) of mounds in the shade and in the open from Sahel and Sudan savannah. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mounds of *M. bellicosus* (built directly in the shade of *Azadirachta indica*), those of *Trinervitermes* sp. A (by the side of a shrub) and mushroom shaped mounds of *C. oculatus* mound attached to a shrub (Fig. 2d, e and 2f respectively).

Logistic regression showed that the predictors were statistically significant, $\chi^2(1, N = 270) = 4.925, p \leq 0.026$, indicating that

Table 2
Percentage (%) of shade and open mounds by species from Sahel and Sudan savannah.

Species (n = Sahel, Sudan)	Sahel		Sudan	
	Shade	Open	Shade	Open
<i>Amitermes</i> sp. (2,2)	100%	0%	0%	100%
<i>C. oculatus</i> (28,4)	50%	50%	75%	25%
<i>M. bellicosus</i> (20,10)	90%	10%	80%	20%
<i>M. subhyalinus</i> (74,46)	80%	20%	80%	20%
<i>Odontotermes</i> sp. (4,2)	75%	25%	100%	0%
<i>Trinervitermes</i> sp. A (5,61)	60%	40%	30%	70%
<i>Trinervitermes</i> sp. B (2,10)	50%	50%	40%	60%

temperature do affects the citing of the mound either in the shade or in the open. Results obtained showed a significant difference ($p < 0.05$) from mounds found in the shade and in the open from the two savannah. Percentage of mounds found in the shade and in the open from Sahel and Sudan savannah are shown in Fig. 3 and Table 2. All mounds belonging to *Amitermes* sp. from the Sahel were found in the shade, while those from the Sudan were in the open (Table 2). *C. oculatus* from Sahel did not display any preferences for locating their mounds either in the open or in the shade (Table 2), but shows preferences for the shade in the Sudan savannah (Table 2). *M. bellicosus* and its sister species *M. subhyalinus* both prefer building their mounds in the shade irrespective of the savannah type (Table 2). *Trinervitermes* sp. A

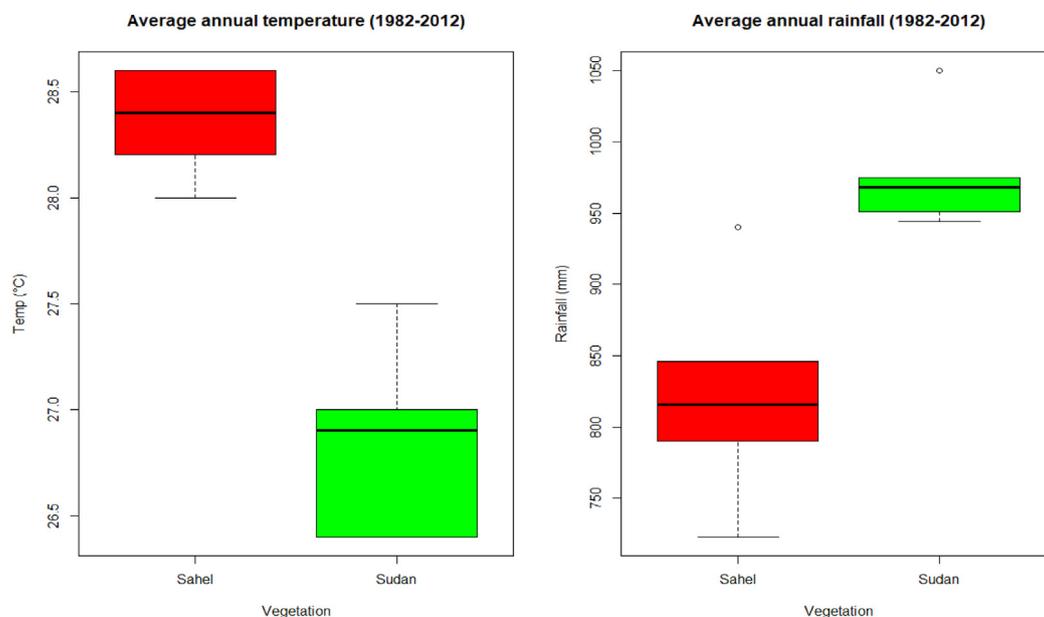


Fig. 4. Long term (1982 and 2012) average ambient temperature and rainfall from Sahel and Sudan savannah. Box shows inter quartile range, circle represents outliers and middle line represent the median, lower and upper whiskers are the lowest and highest values respectively.

Table 3
Mean (\pm SD) internal and ambient temperature of termite mounds from Sahel and Sudan savannah.

Species	Internal Temp.(°C)		Ambient Temp.(°C)	
	Sahel	Sudan	Sahel	Sudan
<i>Amitermes</i> sp.	26.3(\pm 2.8)	29.3(\pm 1.8)	26.0(\pm 2.8)	27.3(\pm 0.9)
<i>C. oculatus</i>	38.7(\pm 3.7)	30.3(\pm 0.7)	38.8(\pm 4.1)	29.8(\pm 0.5)
<i>M. bellicosus</i>	35.2(\pm 4.5)	32.6(\pm 2.0)	34.9(\pm 5.0)	32.1(\pm 1.7)
<i>M. subhyalinus</i>	33.3(\pm 6.4)	33.1(\pm 3.8)	33.4(\pm 5.3)	32.9(\pm 4.7)
<i>Odontotermes</i> sp.	25.1(\pm 17.0)	34.3(\pm 5.7)	34.1(\pm 3.0)	33.8(\pm 5.4)
<i>Trinervitermes</i> sp. A	34.4(\pm 5.7)	34.0(\pm 5.3)	33.7(\pm 5.3)	33.9(\pm 5.1)
<i>Trinervitermes</i> sp. B	28.0(\pm 0.7)	29.4(\pm 4.5)	27.1(\pm 0.1)	29.3(\pm 4.3)

Sample size same as Tables 1 and 2 above.

displayed preferences for nesting in the shade in the Sahel and in the open in Sudan savannah (Table 2). *Trinervitermes* sp. B showed no preferences for nesting site in the Sahel but preferred nesting in the open in Sudan savannah (Table 2).

4. Mounds' internal and ambient temperatures

In Sahel *C. oculatus* mounds had the highest mean internal temperature (\pm SD) and showed the lowest deviation from ambient (Table 3), whereas *Odontotermes* sp. had the lowest internal temperature (\pm SD) and deviated the most from ambient. In the Sudan savannah, *Odontotermes* sp. had the highest and *Amitermes* sp. the lowest average internal temperature, while *Trinervitermes* sp. A showed the highest ambient temperature in Sudan whereas *Amitermes* sp. showed the lowest deviation. Lower mean ambient temperatures were recorded from the two savannahs when compared with the mean internal temperature of the species.

Despite variations in the long time ambient temperatures and rainfall from the two savannah, the internal mound temperatures of all the seven species were not significantly different from the two savannah with *Amitermes* sp. ($p = 0.57$), *C. oculatus* ($p = 0.529$), *M. bellicosus* ($p = 0.682$), *M. subhyalinus* ($p = 0.779$), *Odontotermes* sp. ($p = 0.607$), *Trinervitermes* sp. A ($p = 0.689$) and *Trinervitermes* sp. B ($p = 0.688$). There was no significant difference on the ambient temperature measured at the time of sampling from the two savannah ($t^{258} = -0.8271$, $p = 0.4086$) (Table 3), on the contrary the long-time annual average ambient temperature and rainfall (1982 and 2012) for Sahel and Sudan were significantly different ($t^8 = 6.4117$, $p = 0.0002$) and ($t^8 = -3.8332$, $p = 0.0050$) (Fig. 4) respectively.

5. Discussion

We recorded seven species of mound building termites from five genera within our study area in the two savannah. These genera were similar to what was reported by Meyer et al. (1999) and (Davies et al., 2014) from savannahs in the Kruger National Park South Africa. In terms of species composition we found; *Amitermes* sp., *C. oculatus*, *Odontotermes* sp. and two species of *Trinervitermes* (*Trinervitermes* sp. A and *Trinervitermes* sp. B) and *M. bellicosus*, *M. subhyalinus*. Like in most studies on Afro-tropical termite species (Davies et al., 2014), we were unable to assign names to some species. This is due to the lack of reliable species-specific keys and taxonomic revisions which is a big impediment to ecological research (Korb et al., 2019).

Cathedral, cone, dome and mushroom shape mounds were the major type of mounds built by the termites in the two savannah. The mounds are used as passive means of temperature regulation together with the location where they are built (Grassé and Noirot, 1961). Their shape and position reflects the response of the termites to long-term environmental conditions they experienced. *Odontotermes* sp. and *C. oculatus* had the lowest and highest mean internal temperatures from

Sahel respectively while *Amitermes* sp. and *Odontotermes* sp. from Sudan had the lowest and highest mean internal temperatures respectively. Majority of the termite mounds from the two savannah were found in the shade (Fig. 3 and Table 2) indicating the importance of shade as a passive form of thermal regulations.

We found most of termite mounds in the shade as against the open indicating preferences for nesting sites. Constructing mounds under the shade is said to be a strategy that termites of the savannah use for passive thermoregulation so that they can be shielded from heat and solar radiation (Korb and Linsenmair, 1998a; Lee and Wood, 1971). Similarly, nest site selection, nest orientation and nest architecture are the primary mechanisms used by social insects to regulate microclimatic conditions within their nests (Jones and Oldroyd, 2006). For mounds in the shade (attached to bushes or shrubs), are protected from the intense heat during the day while those directly in the shade receive cover when the sun is at its peak there by limiting their exposure (Korb and Linsenmair, 1998a). Our result showed that termites from the Sahel which records more average temperature and less rainfall (1982 and 2012) happens to have more termites mounds in the shade than in the open while Sudan which records low temperature and more rainfall records less mounds in the shade when compare to the Sahel, which suggest that termites uses the shade as a way of passive thermal regulation.

Temperature was used as the predictor and logistic model was fitted to the data to test the research hypothesis regarding the likelihood that termites build mounds in shaded habitats as a form of thermoregulation. The result showed that as predicted more mounds are built in the shade from the two savannah (Sahel and Sudan) (Table 2), with more of the built mound in warmer habitat (Sahel). According to the model, chances of mound build in the shade are higher in areas of high temperature. In other words, the higher the temperature, the more likely it is that mounds will be built in the shade as a form of temperature control strategy by the termites.

Shapes of mound play a vital role in temperature regulations in termites (Willmer, 1982). Cathedral, cone, dome and mushroom shape mounds were the major type of mounds built by the termites in the two savannah. The mounds are used as passive means of temperature regulation together with the location where they are built (Grassé and Noirot, 1961). Their shape and position reflects the response of the termites to long-term environmental conditions they experienced. Since all of the mushroom shape mounds belonging to *C. oculatus* are in the Sahel (Table 1) and 50% (Table 2) in the open, these might suggest that the mushroom shape serve as a sun umbrella shielding the mound from direct sunlight. Previously, mushroom shape mounds were associated with protection against rainfall (Pearce, 1997; Emerson, 1938, 1956), however, in our study mushroom shape mounds of *C. oculatus* were found in areas with less rainfall and higher ambient temperature (Fig. 4), suggesting that this particular shape can serve a dual purpose of protections against rainfall as well as ambient temperature.

Nest architecture is one way in which temperature regulation is achieved in termite nests as seen in different species (Lüscher, 1961). A number of these structural modifications and or adaptations contributes to temperature regulation. Some mounds of *Amitermes* sp. are fairly spherical (cone and dome) built in the shade or in the open, and consist of irregular thin walled cavities connected by narrow passages, which reduces the flow of temperature out of the mound (Korb and Linsenmair, 2000). Fluctuations in internal temperature in this type of mounds are nearly as great as those of ambient temperature (Korb and Linsenmair, 2000). The thick outer wall combined with location in a shady place, often around tree bases, results in a fairly constant temperature in the nest (Korb and Linsenmair, 1998a; Lüscher, 1961). The greatest degree of homeostasis are in the mounds of Subfamily Macrotermitinae (*Macrotermes* and *Odontotermes* species) where the wall of the nest is up to 60 cm thick and forms very effective insulation (Lüscher, 1961).

Though the current studies looked in to the mound structure and

location as a means of thermal regulations by termites of the savannah, other studies also showed another strategy adapted for thermal regulation within the mound used by some termite species is to actively move to the side/area within a mound which provided the most suitable temperature (Howse, 1970; Samuel et al., 2017; Geyer, 2003). Cabrera and Kamble (2001) and Cabrera and Rust (1996) find out that migration within the nest is used by some termites to track the best brood rearing temperatures. Klingner et al. (2005) and Tracy (1976) also reported one of the active mechanism of termites who nest in the open to prevent overheating by going deep down the soil to obtained water to cool the internal temperature of the mound in the form of evaporative cooling.

Despite these differences in the long time ambient conditions termites were able to keep their internal temperature within the requirements of the colony. *M. bellicosus*, *M. subhyalinus* and *Odontotermes* sp. recorded a high number of mounds in the shade from both the two savannah (Table 1). One of the reasons for this is because these species cultivate fungus gardens that requires a certain level of temperature to be maintained in order to rear the needed *Termitomyces* species (Rouland-lefèvre et al., 2006; Wood and Thomas, 1989). From the results obtained all the seven species found from the two savannah showed no significant difference in their internal nest temperature irrespective of the ambient temperature, this suggest the ability of the termites to maintained the temperature they required within their mound despite the differences in the ambient temperature. Furthermore Korb and Linsenmair (2000) state that, the size of the colony, its rate of metabolic and respiratory activities by both the termites and the reared fungi in the mounds helps in maintaining constant nest temperatures.

There were no significant difference in the internal mound temperature of *Amitermes* sp., *Trinervitermes* sp. A and B from both savannah despite the variations in the ambient temperature. The mode of feeding in termites generally also plays an important role in facilitating how termites regulate their internal mound temperatures (Sugimoto et al., 2000; Bignell and Eggleton, 2000). *Amitermes* sp. consume a variety of foods from relatively sound or decayed wood to grass or fine vegetables debris including dung (Miller, 1994; Ferrar and Watson, 1970) and therefore microbes are needed in the decomposition process of the wood and these microbes usually have a required temperature for them to function at best (Gautam and Henderson, 2011). Therefore, it would be adaptive if the termites provide the general condition for them to survive and decompose. Irrespective of the habitat and environmental conditions the requirements of the microbes to be fulfilled, therefore *Amitermes* sp. needs to make the mound conducive for both the microbes and the termites themselves (Rouland-lefèvre et al., 2006; Becker, 1975; Sands, 1969), which might be the reason for the termites maintaining a similar temperature in both savannah. Likewise, *Trinervitermes* sp. A and B are grass feeders and they have to keep the temperature ideal for the grass to decompose in order to achieve that the termites has to maintained a constant internal nest temperatures. *Trinervitermes* species usually collect and store grasses in their nest, the stored grasses and the soil microbes in the mounds need a certain temperature to stay in good state for a longer period in addition to keeping the delicate body of the termites moist. With raising mound temperatures the stored grasses serve also as insulators and a buffer to the termites (Heinrich, 1993).

Similarly there were no significant difference in the internal mound temperature of *C. oculatus* from the two savannah of the study area which shows how temperature regulation plays a role in the mounds of this species. This might also be attributed to the nature of feeding (soil/humus feeders) as earlier mentioned, though these species do not rear fungi in their mounds which needs optimal temperature not withstanding they also need a stable temperature to keep both their body and their juveniles moist at all times which might have brought about the same internal temperature from the two savannah (Ndiaye et al., 2004; Foley et al., 2018).

The way termites always maintained the temperature within their

mounds and how this happens has always been at the forefront of most termite research. The result showed no significant difference on the immediate measured ambient temperature but long term ambient monitored temperature and rainfall (1982 and 2012) of Sahel and Sudan were significantly different (Fig. 4), the observed mound shapes, locations and internal temperatures might reflect long term cumulative responses of the termites to the environmental conditions. We have shown that, irrespective of location or ambient temperature termites do maintained internal temperatures within limits that is required for the nest to function. All the species found in the study area showed no significant difference in their internal mound temperature. *M. bellicosus*, *M. subhyalinus* and *Odontotermes* sp. were the three species that showed more affinity towards the shade. Building mushroom/umbrella shape mound by *C. oculatus* as a passive means of thermal regulation which was before now believed to be exclusively for protection against rainfall. Since the presence of soil microbes or other soil arthropods are influential in maintaining mound temperatures. There is the need to explore this by characterising soil microbes and arthropods associated with each termite species and habitat.

Acknowledgements

We thank, Prof. Robin Crewe, Dr. Jannette Mitchell and colleagues from the Social Insects Research Group (SIRG) for their valid discussions and contributions to this work. We also thank Prof. Judith Korb for providing the keys used for the identification of *Macrotermes* and *Cubitermes*. Funding for this research was provided in part by: The University of Pretoria, The South African National Research Foundation (NRF) Incentive Funding for Rated Researchers (IFRR) to CWWP and Y-Rated Research Grant and Thuthuka (Rating Track) to AAY. IPA was supported by a University of Pretoria Postgraduate Bursary and the Nigerian Tertiary Education Trust Fund (TETFund).

References

- Abe, S.S., Yamamoto, S., Wakatsuki, T., 2009. Soil-particle selection by the mound-building termite *Macrotermes bellicosus* on a sandy loam soil catena in a Nigerian tropical savanna. *J. Trop. Ecol.* 25, 449–452.
- Becker, G., 1975. Termites and fungi. *Mater. Org. (Berl.)* 30, 465–478.
- Bignell, D.E., Eggleton, P., 2000. Termites in ecosystems. In: *Termites*.
- Buckley, L.B., Miller, E.F., Kingsolver, J.G., 2013. Ectotherm thermal stress and specialization across altitude and latitude. *Integr. Comp. Biol.* 53, 571–581.
- Cabrera, B.J., Kamble, S.T., 2001. Effects of decreasing thermophotoperiod on the Eastern subterranean termite (Isoptera: Rhinotermitidae). *Environ. Entomol.* 30, 166–171.
- Cabrera, B.J., Rust, M.K., 1996. Behavioral responses to light and thermal gradients by the Western drywood termite (Isoptera: Kalotermitidae). *Environ. Entomol.* 25, 436–445.
- Climate-dataORG <https://en.climate-data.org/location/398004/climate-data.org>.
- Collins, M.N., 1979. The Nests of *Macrotermes bellicosus* (Smeathman) from Mokwa, Nigeria.
- Collins, N.M., 1981. The role of termites in the decomposition of wood and leaf litter in the Southern Guinea Savan. *Oecologia (Berl.)* 51, 389–399.
- Dahlsjö, C.A., Parr, C.L., Malhi, Y., Meir, P., Eggleton, P., 2015. Describing termite assemblage structure in a Peruvian lowland tropical rain forest: a comparison of two alternative methods. *Insectes Sociaux* 62, 141–150.
- Danks, H.V., 2002. Modification of adverse conditions by insects. *Oikos* 99, 10–24.
- Davies, A.B., Levick, S.R., Asner, G.P., Robertson, M.P., Rensburg, B.J.V., Parr, C.L., 2014. Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography* 37, 852–862.
- Emerson, E.A., 1938. *Termite Nests—A Study of the Phylogeny of Behavior*. Ecological Monographs 8, 247–284.
- Emerson, A.E., 1956. Regenerate Behavior and Social Homeostasis of Termites. *Ecology* 37, 248–258.
- Erpenbach, A., Wittig, R., 2016. Termites and savannas—an overview on history and recent scientific progress with particular respect to West Africa and to the genus *Macrotermes*. *Flora et Vegetatio Sudano-Sambesica* 19, 35–51.
- Ferrar, P., Watson, J., 1970. Termites (Isoptera) associated with dung in Australia. *Aust. J. Entomol.* 9, 100–102.
- Foley, J.R.T., Chouvenet, T., Giblin-davis, R.M., Su, N.Y., Kanzaki, N., 2018. Phoresy and within-colony transmission of nematodes associated with alates of subterranean termites (Isoptera: Rhinotermitidae). *Environ. Entomol.* 47, 1107–1116.
- Fuchikawa, T., Matsubara, K., Miyatake, T., Matsuura, K., 2012. Acoustic emission monitoring of the effect of temperature on activity rhythms of the subterranean termite *Reticulitermes speratus*. *Physiol. Entomol.* 37, 303–308.
- Gautam, B.K., Henderson, G., 2011. Wood consumption by Formosan subterranean

- termites (Isoptera: Rhinotermitidae) as affected by wood moisture content and temperature. *Ann. Entomol. Soc. Am.* 104, 459–464.
- Geyer, J.W., 2003. A comparison between the temperatures in a termite supplementary fungus garden and in the soil at equal depths. *J. Entomol. Soc. South. Afr.* 14, 36–43.
- Grassé, P.-P., Noirot, C., 1961. Nouvelles recherches sur la systématique et l'éthologie des Termites champignonnistes du genre *Bellicositermes* Emerson. *Insectes Sociaux* 8, 311–359.
- Heinrich, B., 1993. *The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation*. Harvard University Press, Cambridge, Mass.
- Howse, P.E., 1970. *Termites: a Study in Social Behaviour*. Hutchinson, London.
- Huey, R.B., Hertz, P.E., Sinervo, B., 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* 161, 357–366.
- Jones, J.C., Oldroyd, B.P., 2006. Nest thermoregulation in social insects. In: Simpson, S.J. (Ed.), *Advances in Insect Physiology*. Academic Press.
- Jouquet, P., Guilleux, N., Shanbhag, R.R., Subramanian, S., 2015. Influence of soil type on the properties of termite mound nests in Southern India. *Appl. Soil Ecol.* 96, 282–287.
- Klingner, R., Richter, K., Schmolz, E., Keller, B., 2005. The role of moisture in the nest thermoregulation of social wasps. *Naturwissenschaften* 92, 427–430.
- Kofoed, C.A., 1934. *Termites and Their Control*.
- Korb, J., Kasseney, B.D., Cakpo, Y.T., Casalla DAZA, R.H., Gbenyedji, J.N.K., Ilboudo, M.E., Josens, G., Meusemann, K., Ndiaye, A.B., Okweche, S.I., 2019. Termite taxonomy, challenges and prospects: west Africa, a case example. *Insectes* 10, 1–8.
- Korb, J., Linsenmair, K.E., 1998a. The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna. *Insectes Sociaux* 45, 51–65.
- Korb, J., Linsenmair, K.E., 1998b. Experimental heating of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds: what role does microclimate play in influencing mound architecture? *Insectes Sociaux* 45, 335–342.
- Korb, J., Linsenmair, K.E., 1999. Reproductive success of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) in two neighbouring habitats. *Oecologia* 118, 183–191.
- Korb, J., Linsenmair, K.E., 2000. Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? *Insectes Sociaux* 47, 357–363.
- Korb, J., Linsenmair, K.E., 2000a. Ventilation of termite mounds: new results require a new model. *Behav. Ecol.* 11, 486–494.
- Lee, K.E., Wood, T.G., 1971. *Termites and Soils*. Academic Press, London.
- Lüscher, M., 1956. Die Lüfterneuerung im nest der termite *Macrotermes natalensis* (Haviland). *Insectes Soc.* 3, 273–276.
- Lüscher, M., 1961. Air-conditioned termite nests. *Sci. Am.* 205, 138–145.
- Meyer, V., Braack, L., Biggs, H., Ebersohn, C., 1999. Distribution and density of termite mounds in the northern Kruger National Park, with specific reference to those constructed by *Macrotermes Holmgren* (Isoptera: Termitidae). *African Entomology* 7, 123–130.
- Miller, L., 1994. *Amitermes arboreus* Roisin in Australia, with notes on its biology (Isoptera: termitidae). *Aust. J. Entomol.* 33, 305–308.
- Ndiaye, D., Lensi, R., Lepage, M., Brauman, A., 2004. The effect of the soil-feeding termite *Cubitermes niokoensis* on soil microbial activity in a semi-arid savanna in West Africa. *Plant Soil* 259, 277–286.
- Noirot, C., Darlington, J.P.E.C., 2000. Termite nests: architecture, regulation and defence. In: Abe, T., Bignell, D.E., Higashi, M. (Eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*. Springer Netherlands, Dordrecht.
- Ola-adams, B.A., Iyamabo, D.E., 2009. Conservation of natural vegetation in Nigeria. *Environ. Conserv.* 4, 217–223.
- Orhue, E.R., Uzu, F., Osaigbovo, A., 2007. Influence of Activities of Termites on Some Physical and Chemical Properties of Soils under Different Land Use Patterns: A Review.
- Pearce, M.J., 1997. *Termites, Biology and pest management*. Ecology, Willing Ford United Kingdom.
- Rouland-lefevre, C., Inoue, T., Johjima, T., 2006. Termitomyces/termite interactions. In: König, H., Varma, A. (Eds.), *Intestinal Microorganisms of Termites and Other Invertebrates*. *Soil Biology*, vol. 6. Springer, Berlin, Heidelberg, pp. 335–336.
- Ruelle, J.E., 1970. Revision of the termites of the genus *Macrotermes* from the Ethiopian region (Isoptera: termitidae). *Br. Mus. Nat. Hist. Bull. Entomol.* 365–444.
- A. O. Samuel, King, Hunter, Andreen, David, Bardunias, Paul, Turner, J.Scott, Soar, R., Mahadevan, L., 2017. Solar-powered ventilation of Africa n termite mounds. *J. Exp. Biol.* 220, 3260–3269.
- Sands, W.A., 1969. The association of termites and fungi. *Biol. Termites* 1, 495–524.
- Sponsler, R.C., Appel, A.G., 1991. Temperature tolerance of formosa and eastern subterranean termites. *J. Therm. Biol.* 16, 41–44.
- Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* 17, 866–880.
- Sugimoto, A., Bignell, D.E., Macdonald, J.A., 2000. Global Impact of Termites on the Carbon Cycle and Atmospheric Trace Gases. *Termites: Evolution, Sociality, Symbioses, Ecology*. Springer.
- Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey, R.B., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl. Acad. Sci.* 111, 5610–5615.
- Tracy, C.R., 1976. A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. *Ecol. Monogr.* 46, 293–326.
- Vivienne, U., 2002. *A Guide to the Termites Genera of of Southern Africa*. A plant protection research institute handbook, pp. 1–116.
- Willmer, P.G., 1982. Microclimate and the environmental physiology of insects. In: Berridge, M.J., Treherne, J.E., Wigglesworth, V.B. (Eds.), *Advances in Insect Physiology*. Academic Press.
- Wood, T.G., Thomas, R.J., 1989. *The Mutualistic Association between Macrotermitinae and Termitomyces*. Academic Press, London.
- Woon, J.S., Boyle, M.J.W., Ewers, R.M., Chung, A., Eggleton, P., 2019. Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests. *Insectes Sociaux* 66, 57–64.
- Yusuf, A.A., Gordon, I., Crewe, R.M., Pirk, C.W.W., 2014. Prey choice and raiding behaviour of the Ponerine ant *Pachycondyla analis* (Hymenoptera: Formicidae). *J. Nat. Hist.* 48, 345–358.