

Comparison of nest shapes and densities of two sympatric species of *Cubitermes* (Isoptera: Termitidae: Termitinae) as clues for the study of their population dynamics

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Two species of *Cubitermes* coexist in the grassy *Loudetia* Savanna of Bondoé, in the Central African Republic, namely *C. sankurensis* (Wasmann, 1911) and *C. ugandensis* (Fuller, 1923). Despite the obvious size difference between individuals their nests have the same general shape but there are significant, though small, differences in height, diameter, number of caps, surface and volume. The closest correlations between these five parameters can be seen between the surface and the volume of the nests. The regressions between these two parameters are identical for both species; the addition of a first cap decreases the volume/surface ratio but a second or third cap does not alter this ratio further. Three apparent age classes have been attributed to the nests based on their external appearance: recent, eroded, and dilapidated. The great density (1297 nests/ha) and abundance of the nests that are dilapidated but still occupied by a declining population clearly suggests that the pressure from predation is weak. This study suggests that the environmental conditions are more influential than the species in shaping the mounds and tentative population dynamics of the termite mounds of Bondoé are outlined.

Key words: humivorous termites, mound density, Central Africa.

INTRODUCTION

The *Cubitermes* (Isoptera: Termitidae: Termitinae) are a type of termite that is endemic to Africa, and its epigeic, mushroom-shaped nests are typical of certain landscapes (Grassé 1984; Eggleton 2000); they inhabit diverse environments ranging from rainforest to Sudanese savannas (Williams 1966).

The epigeal part of the nest consists of faeces and soil (Wood 1988; Brauman *et al.* 2000). Its shape varies among species and environments, ranging from a simple dome to columns existing singly or side by side and often topped by one or several caps (Williams 1966).

The internal structure consists of rooms separated by thin walls and communicating with each other through openings whose diameter matches the head size of the soldiers. This architecture allows the diffusion (not the convection) of respiratory gases and plays an important role in the static defence against predators (Deligne & Pasteels 1982) while ensuring good connectivity (Perna *et al.* 2008).

Because of their construction activities, the *Cubitermes* deserve to be called 'ecosystem engineers' since they create structures that influence other organisms; they change the physical and chemical properties of the soil, improving drainage and soil aeration (Quantin 1965; Wood 1988). Indeed *Cubitermes* termite mounds often accommodate other species of termites (Dejean & Ruelle 1995), inquilines and competitors that coexist with the builders, or secondary occupants that take over the nest after the death of the builders (Bodot 1967).

Although their nests are usually easily visible, *Cubitermes* have been little studied, probably because they are humivores who pose no problem either to agriculture or construction (Maldague 2003). The growth of their populations is still poorly understood and the dynamics of the populations of their nests, briefly discussed in Bouillon & Lekie (1964), are known only in regard to two species: *C. fungifaber* (Han & Lepage 1991) and *C. speciosus* (Soki *et al.* 1996).

Two or more species of *Cubitermes* often coexist

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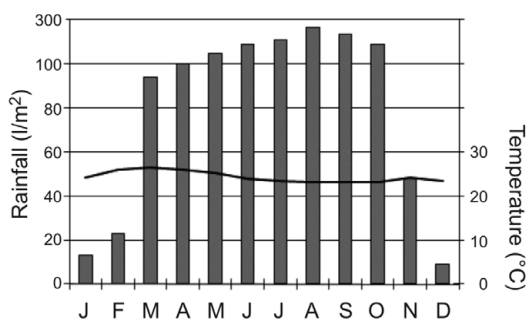


Fig. 1. Ombrothermic diagram of the town of Bossembélé. Note: the scale of precipitation is divided by 10 for values above 100 l/m².

in the same environment (Williams 1966) and this is also the case in the savanna of Bondoé, where two species of high density coexist. Here, we describe the shape and density of the mounds of both species. The relationship between those parameters and the population dynamics of the mounds is also discussed. This is also an opportunity to check to what extent Williams' claim of likeness of the mounds of two *Cubitermes* species is true when they are sympatric.

MATERIALS & METHODS

Geographic location and site selection

The study was conducted in the Central African Republic near the village of Bondoé, 142 km northwest of Bangui. The site (5°10'N, 17°44'E) was chosen because of the abundance of termite mounds established on lateritic soil, which allows the population of the termite mounds to be monitored for years without much fear of the site being brought under cultivation.

Climate

The meteorological data come from the station at Bossembélé, 15 km from Bondoé. The climate is tropical with a rainy season from March to November and a dry season from December to February (Fig. 1). The region receives on average 1510 mm of rain per year and the average annual temperature is around 24.2°C (Weatherbase 2010).

Topography and vegetation

On satellite photographs, the vegetation of the region appears as a mosaic of forested galleries and savannas. The site where the work was done is on a plateau situated at about 700 m in altitude and in a slight depression. It gives the impression

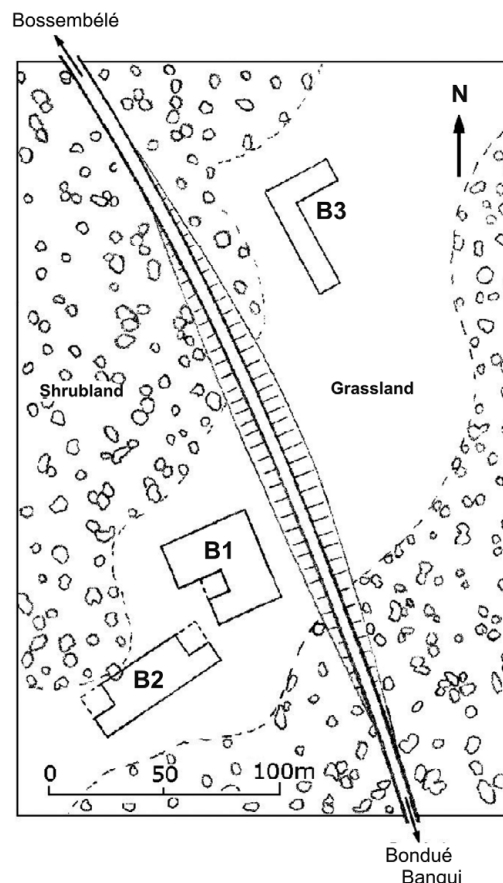


Fig. 2. Map of the study site crossed by the road RN1. The dotted lines mark the plots whose mounds were not identified (see text).

of a 'valley' very open, about a hundred metres wide and with hardly any slope. It is on a transhumance track used by herds of cattle moving from Chad to Cameroon. The soil rests on a crust of laterite (bowal) which outcrops in places. It is shallow but local small beaches a few square metres in size offer deeper patches of soil. Its average depth is 17.2 ± 8.3 cm, $n = 57$; this was measured by inserting a metal rod into the ground until it struck the crust. The RN1 road crosses the 'valley' on an embankment and divides the site into two (Fig. 2).

The bottom of the 'valley' of the site is occupied by a grassland dominated by *Loudetia arundinacea* and is surrounded by shrublands whose grassy carpet is dominated by *Hyparrhenia* spp. and *Imperata cylindrica*. The shrub layer includes shrubs of the genera *Vitex*, *Bridelia* and *Terminalia*. Following heavy rains, the bottom of the 'valley' is

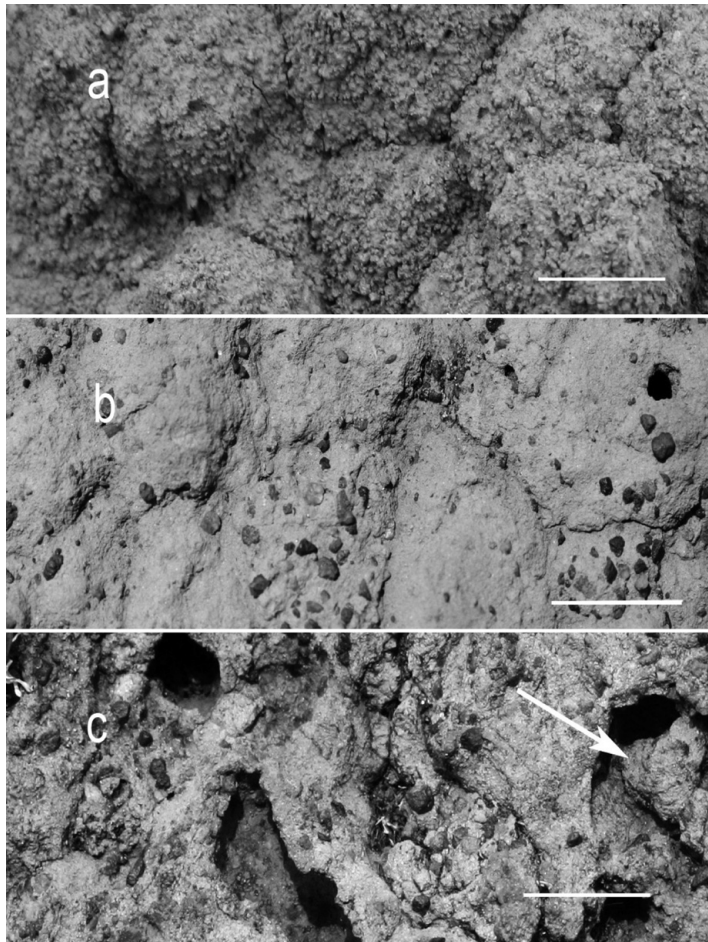


Fig. 3. Appearance of the surface of the nest: **a**, the lumpy surface of a recent nest with the outline of cells easily visible; **b**, the smoother surface and visible lateritic grains of sand of an eroded nest: the outline of the cells is still visible and one of them is perforated (right); **c**, the heavily eroded surface of a dilapidated nest: more cells are perforated and some have been filled with earth (arrow). Scale bars = 1 cm.

occasionally flooded for several hours and the soil remains waterlogged for a long time, with a gradient from southwest (drier) to northeast (wetter).

Delineation of permanent plots

Plots sized 10×10 m were marked off in homogeneous grassland without lateritic outcrops. They were accurately measured using a laser range-finder and marked off with iron stakes driven into the ground and stabilized with cement. They will remain in place for several years in order to carry out experiments and monitor the dynamics of the termite mounds they contain. A total of 33 plots is arranged in three blocks of 14, 12 and 7 plots. Blocks B1 and B2 are to the southwest of the road and block B3 is to the northeast (Fig. 2).

Description of termite mounds

The observations were made in April 2006 in blocks B1 and B2, and in April 2007 in Block B3, that is to say, in all cases at the beginning of the rainy season. For each termite mound, a record was created, including a sketch, measurements and its apparent age (recent, eroded or dilapidated) from the appearance of its surface.

A recent nest is characterized by the absence of holes in the cap and, at least in some places, its grainy surface due to the presence of small pellets recently deposited by workers during construction. Large sand grains incorporated in construction are still coated with clay and are not visible, while the contours of the cells are clearly visible (Fig. 3a). A nest is said to be eroded when the cap surface is

relatively smooth, the grains of lateritic sand have been washed clean of the clay that covered them and are clearly visible. A few holes are observed resulting from erosion having pierced the walls of some rooms, the outline of cells is still visible, but is beginning to fade (Fig. 3b). Finally a dilapidated nest also shows washed grains of sand that are visible at the surface; in addition, the outline of the cells is no longer visible and many holes are present, some of which open onto rooms that have been largely filled in with earth (Fig. 3c).

The spatial coordinates of the nests were also noted, but this part of the study will be published elsewhere.

Sampling termites

The termites were found by taking successive fragments of the nest until at least one *Cubitermes* soldier was collected. During this process of collection, the interior appearance of the nest (presence of filled cells) and the type of population (abundance of larvae, the presence of inquilines) were noted. Identification of termites was conducted using the identification keys of Sjöstedt (1926), Williams (1966) and Bouillon & Mathot (1965).

Estimation of the volume and surface of the nest

As described in Soki & Josens (1996), the volume and surface area of *Cubitermes* termite mounds can be estimated by approximating their shape to that of stacks of cylinders, cones and trunks of cones. The total volume of a nest is thus the sum of the volumes of the different parts of the nest; the same applies to the total area but after deducting the area located at the intersection of the stacked geometric shapes.

All measurements necessary to calculate the volume and external surface of the nests (circumferences and heights) were made using a tape measure with an accuracy of ± 1 cm.

Statistical analysis

Analysis of results was made considering the *Cubitermes* species, the blocks and the apparent age of the nests. The numbers of nests per plot and the measurements of height, diameter, surface and volume were normalized by logarithmic transformation and compared by ANOVAs followed by Tukey tests for unequal sample sizes using the software Statistica® 8. The number of caps, however, could not be normalized and these were compared using Kruskal-Wallis and Mann-Whitney tests. The slopes of regression lines and

their y -intercepts were compared by Student's t -tests (Zar 1999). The results are expressed as means \pm standard deviations.

RESULTS

Identification of the termite mounds

A total of 516 termite mounds was counted, of which 428 were occupied by *Cubitermes* spp., on a surface of 3300 m², representing a total density of 1564 nests per hectare, including 1297 that were occupied by their builders. Thus there were 88 nests that were abandoned or unidentifiable, and these were not considered in the subsequent analysis.

Of 428 termite mounds occupied by *Cubitermes*, 375 nests were sampled and identified while 53 (on three plots) were removed without being identified as part of a study of the dynamics of their populations, when we were not yet aware of the presence of the two species. The 391 nests identified comprised 294 nests of *Cubitermes sankurensis* (Wasmann 1911) and 81 nests of *Cubitermes ugandensis* (Fuller, 1923). No nest contained the two species simultaneously, but 129 nests (of 516) harboured at least one other species of termite (68 of them housing only other termites): *Ancistrotermes* (40 occurrences), *Microtermes* (2), *Pseudacanthotermes* (2), *Microcerotermes* (7), *Adaiphrotermes* (24), *Basidentitermes* (2), *Duplidentitermes* (1), *Forficulitermes* (1), *Ophiotermes* (5), *Pericapritermes* (19), *Promirotermes* (22), *Fulleritermes* (2), *Trinervitermes* sp (7), *T. geminatus* (2), *T. oeconomus* (3), *T. togoensis* (3) and indeterminate (5).

The nests of both species of *Cubitermes* exhibit varied external shapes (Fig. 4) ranging from nests that are massive, broad and low (up to 60 cm in diameter and a height of 20 cm) to nests that are more slender (15 cm in diameter and 40 cm in height). The trunk is generally composed of a single column but sometimes has two columns side by side; there are one to five caps whose edges often have long 'fingers' (a drainage device?). A simple visual observation cannot identify a nest as having been built by one or the other species.

Analysis of the assemblage of mounds

The analysis was performed on the 30 plots where the species of *Cubitermes* were identified. The average number of nests per plot (Fig. 5) was compared using a three-way ANOVA (species, block and apparent age). The nests were more

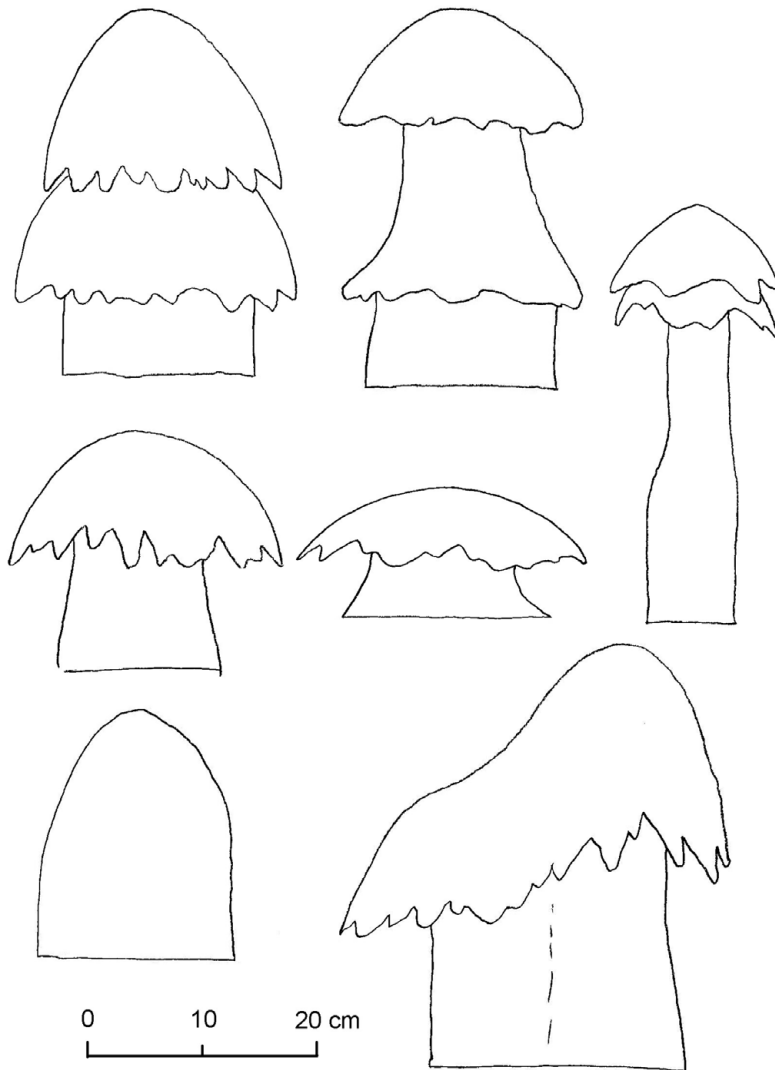


Fig. 4. Line drawings of seven *Cubitermes* nests from Bondoé (all of 'recent' or 'eroded' appearances) showing the variety of shapes independently of the building species; 'dilapidated' nests are not shown, most of them are roughly dome-shaped.

numerous in block B3 (17.9 ± 5.6 per plot) than in blocks B1 (11.7 ± 3.8 per plot) and B2 (9.8 ± 5.4 per plot) (2 d.f., $P = 0.024$); the nests of *C. sankurensis* were significantly more numerous (9.8 ± 5.2 per plot) than those of *C. ugandensis* (2.7 ± 2.3 per plot) (1 d.f., $P < 0.001$) (Fig. 5) and the eroded nests were significantly more numerous (8.4 ± 5.6 per plot) than the dilapidated nests (3.0 ± 2.3 per plot), which themselves outnumbered recent nests (1.1 ± 1.5 per plot) (2 d.f., $P < 0.001$) (Fig. 6).

Significant interactions between blocks, species and apparent ages reflect the facts that (a) there were proportionally more nests of *C. ugandensis*

and fewer nests of *C. sankurensis* in Block B2 than in the other two blocks (2 d.f., $P = 0.02$), (b) there were proportionally more eroded nests of *C. sankurensis* than *C. ugandensis* (2 d.f., $P < 0.001$, Fig. 6) and (c) there were proportionally more eroded nests and fewer dilapidated nests in block B3 than in the other two blocks (4 d.f., $P < 0.003$).

Comparison of nest parameters

Every parameter, but the number of caps, was analysed by a two-way ANOVA (block and species).

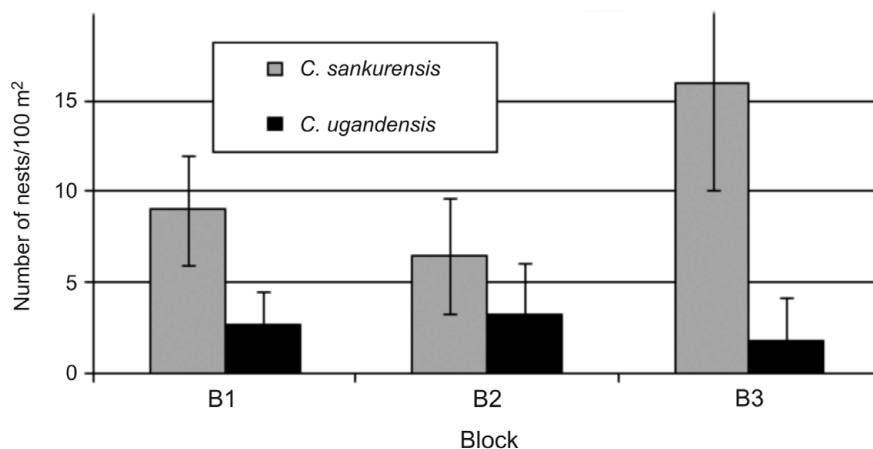


Fig. 5. Number of nests per plot of 100 m² (mean ± standard deviation) based on species and blocks.

Height

The mounds of *C. ugandensis* were significantly higher (35.8 ± 13.4 cm) than those of *C. sankurensis* (31.1 ± 12.0 cm) (1 d.f., $P < 0.001$) and there was a highly significant difference between blocks (2 d.f., $P < 0.001$); the nests of block B2 were significantly lower (29.5 ± 11.6 cm) than those of blocks B1 and B3 (34.6 ± 12.6 cm) (2 d.f., $P < 0.001$). There was no interaction between the two factors.

Diameter near base

There was a highly significant difference between blocks (2 d.f., $P < 0.001$); the mounds of block B2 had a diameter significantly larger (34.0 ± 11.0 cm) than those of blocks B1 and B3 (28.9 ± 11.1 cm) (2 d.f., $P < 0.001$). There was no significant difference between species and no interaction between the two factors.

Surface area

The surface area of the mounds of *C. ugandensis* were significantly larger (43.8 ± 22.4 dm²) than those of *C. sankurensis* (37.6 ± 21.1 dm²) (1 d.f., $P < 0.02$). Between blocks there was no significant difference (2 d.f., $P = 0.76$) and there was no interaction between the two factors (d.f. 2, $P = 0.74$).

Volume

The mounds of *C. ugandensis* were significantly more voluminous (25.3 ± 18.8 dm³) than the nests of *C. sankurensis* (20.8 ± 17.2 dm³) (1 d.f., $P < 0.04$). There was no significant difference between the blocks (2 d.f., $P = 0.11$) and there was no interaction between the two factors (2 d.f., $P = 0.50$).

Number of caps

Over 80% of the nests of both species had one or

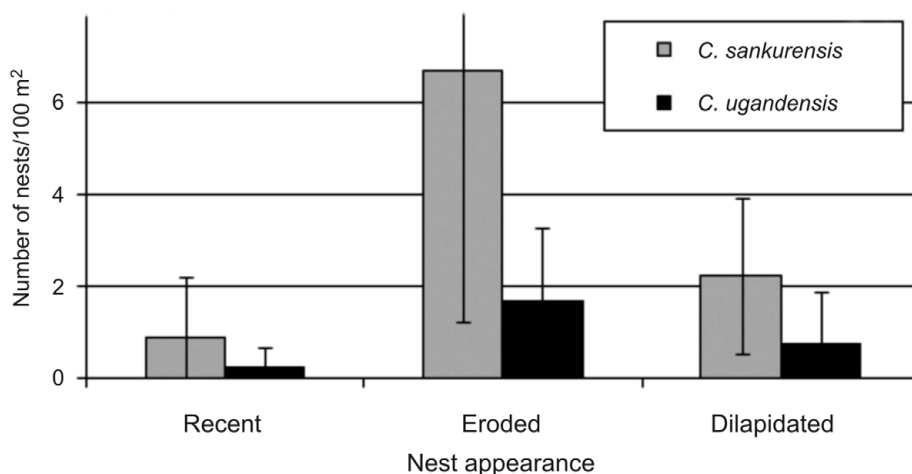


Fig. 6. Number of nests per plot of 100 m² (mean ± standard deviation) based on species and their appearance.

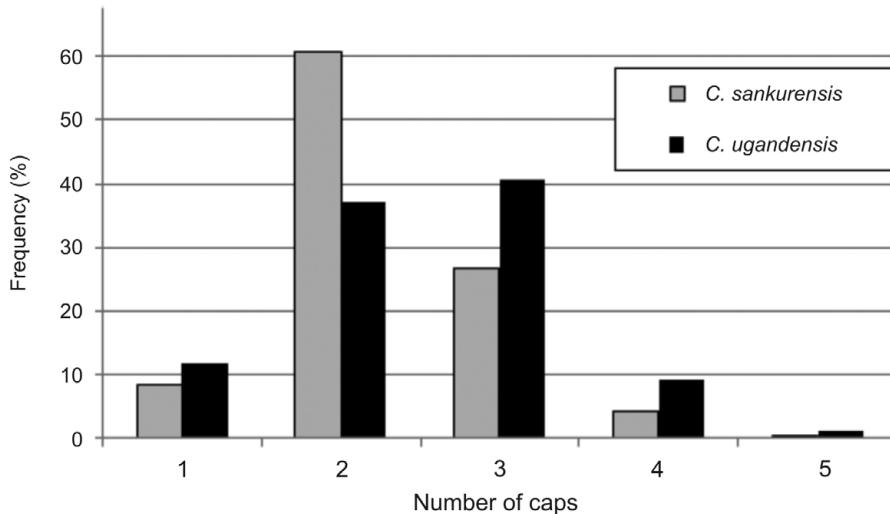


Fig. 7. Distribution of nests of both species based on their number of caps.

two caps and the maximum number observed in Bondoé was five (Fig. 7). The numbers of caps were compared using a Mann-Whitney test. The nests of *C. ugandensis* had significantly more caps (1.5 ± 0.9) than those of *C. sankurensis* (1.3 ± 0.7) ($P < 0.05$). The nests in block B2 had fewer caps than those in blocks B1 and B3 (Kruskal-Wallis, $P < 0.01$).

Massiveness and correlation between nest parameters

There was a highly significant difference in massiveness (ratio diameter/height) between blocks (2 d.f., $P < 0.001$); the mounds of block B2 being significantly more massive ($D/H = 1.33 \pm 0.56$) than those of blocks B1 and B3 ($D/H = 0.95 \pm 0.43$) (2 d.f., $P < 0.001$). There was no significant difference between species and no interaction between the two factors.

The parameters were all highly significantly correlated and the regression lines of the two species were compared: neither their slopes nor

their y -intercept were significantly different (Student's t -test), and both species were thus treated jointly. The strongest correlation was obtained between the surface and volume of the nests (log-transformed) (Table 1) and the correlations involving the height of the nests gave the lowest correlations.

If we represent the correlations of the volume based on the surface, distinguishing the nests according to the number of caps, it was the nests without caps whose regression line had the highest y -interception, indicating that at equal volume, nests with caps have a larger area (Fig. 8). By contrast, the regression lines of nests with one, two or three caps were not statistically different.

DISCUSSION

Sympatric species and competition

The coexistence of at least two species of *Cubitermes* is common, according to Williams (1966). Thus *C. ugandensis* has been found in

Table 1. Correlation between the different parameters of the nests of *Cubitermes sankurensis* and *C. ugandensis* combined ($n = 375$ and $P < 0.01$ in each case).

Dependent variable*	Independent variable*	R^2	Regression equation
Surface	Height	0.57	$y = 1.215x + 1.955$
Volume	Height	0.52	$y = 1.757x + 2.378$
Volume	Surface	0.94	$y = 1.454x - 0.468$
Height	No. caps	0.15	$y = 0.0896x + 0.354$
Surface	No. caps	0.09	$y = 0.116x + 2.377$
Volume	No. caps	0.04	$y = 0.119x + 3.052$

*Heights, surfaces and volumes were log-transformed (base 10).

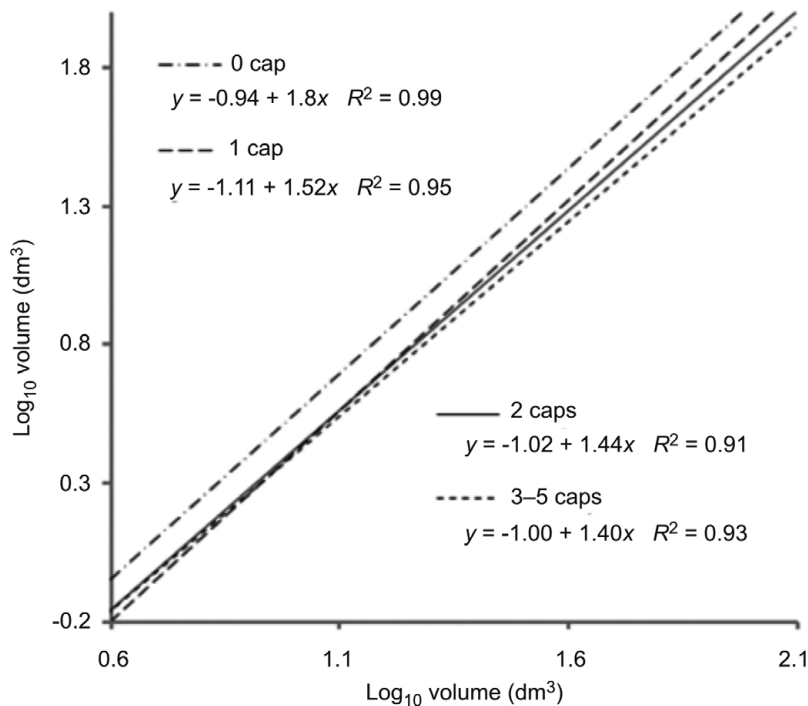


Fig. 8. Regression lines between the volume and surface nests based on the number of caps. The 375 data points of the individual nests are not shown for the sake of clarity.

various localities of East Africa along with eight other species, including *C. sankurensis*, and the latter was found with nine of the 18 species of *Cubitermes* studied by Williams (1966). Our study indicates that the shape of nests of the same species can vary from one locality to another, but in the same locality it is often difficult to distinguish between the nests of two sympatric species, although the termites themselves may be of different sizes.

These findings apply particularly well to the two sympatric species of the Bondoé savanna: the workers of *C. ugandensis* weigh 11.2 ± 1.2 mg and those of *C. sankurensis* weigh 6.9 ± 0.8 mg (average fresh mass of 10 individuals in each case) and the gap is even greater with the soldiers. In agreement with these mass differences, the nests of *C. ugandensis* were statistically larger than those of *C. sankurensis*, but the difference was small and, on the ground, it was impossible to distinguish between the nests of the two species without taking samples. The proportions of nests of both species were so similar that (a) their regression lines (the volume based on the surface or height) could not be statistically differentiated, despite the large numbers studied, (b) their ratio diameter/

height differed between blocks but not between species and (c) the frequency distributions of volumes of nests did not differ (chi-square test, 6 d.f., $P > 0.2$, Fig. 9). By contrast, the frequency distribution of volumes of *C. sankurensis* nests studied by Bouillon & Lekie (1964) in the Democratic Republic of Congo) was totally different, since even the largest of their nests did not reach 17 dm^3 (Fig. 9).

The coexistence of two species of *Cubitermes* would be possible, according to Williams (1966), due to divergent diets, for example by exploitation of different soil horizons; sympatric species would therefore have little or no competition. It is worth mentioning that the two sympatric species of Bondoé have different enteric valves; those of *C. ugandensis* are 'simple' type and those of *C. sankurensis* are the 'asymmetric jaw' type (Bouillon & Vincke 1971, with verification using Bondoé material). These authors hypothesized that the different structures of the enteric valves could be related to their different diets, but this link remains to be established, as indeed does any adaptation of valves to different diets. It is also interesting to recall that *C. ugandensis* has frequently been found in East Africa in the same

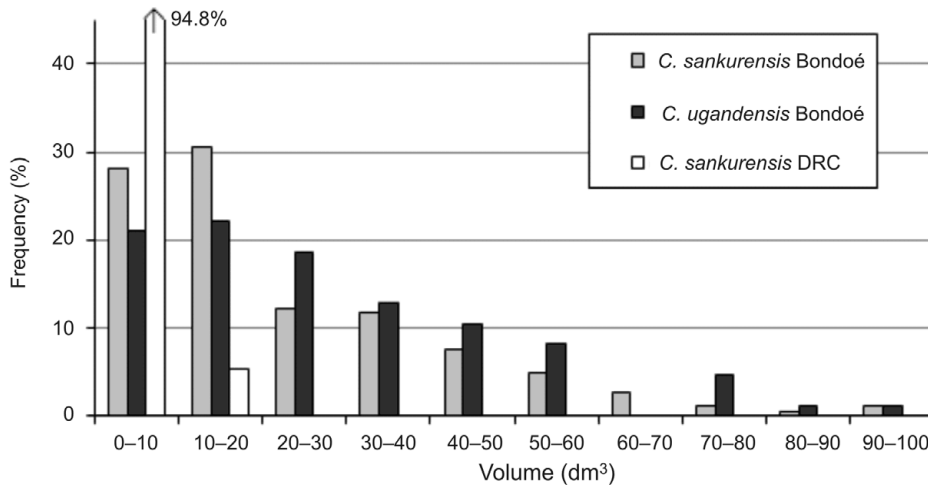


Fig. 9. Distributions of relative frequencies of the volumes of nests of both *Cubitermes sankurensis* and *C. ugandensis* from Bondoé and nests of *C. sankurensis* from the Democratic Republic of Congo to the east of Kinshasa (Bouillon & Lekie 1964).

sites as *C. testaceus*, a species which, like *C. sankurensis*, has an enteric valve of the 'asymmetric jaw' type (Bouillon & Vincke 1971). With regard to the pair *C. ugandensis*–*C. testaceus*, Williams (1966) remarked that the association is neither fortuitous nor temporary.

In our study, it was found that there were proportionally more *C. ugandensis* nests and fewer *C. sankurensis* nests in Block B2 than in the other blocks. This could be an indication of inter-specific competition, but at the scale of the plots of 100 m², there was no negative correlation between the numbers of nests of either species ($r = 0.073$, $n = 30$. $P > 0.50$). Similarly, the failure to find any nest containing simultaneously the two *Cubitermes* species could be interpreted as a sign of exclusion, but this argument is invalid in view of the sampling method used i.e. it was interrupted when one or two *Cubitermes* soldiers had been collected, which almost automatically excluded the possibility of gathering the two species from one nest. Indeed, when some nests were sampled totally (outside of the permanent plots), both species could be found in the same mound (Y. Roisin, pers. comm.). For the same reason, the list of inquiline species or secondary occupants is certainly far from exhaustive.

Apparent age of nests

Bodot (1969) identified three periods (juvenile, adult and senile) in the life of *Cubitermes severus* nests in the savannas of the lower Ivory Coast, based on the number of individuals (juvenile

societies: <10 000 individuals, adults: 10 000 to 40 000, and seniles: >40 000), as well as the proportion of larvae and the capacity to produce alates.

Depending on the appearance of nests of Bondoé, three types were also distinguished: recent, eroded and dilapidated nests. This concerns apparent ages because the freshness of the walls of termite mounds is not strictly related to their actual age and thus only corresponds partially to the periods defined by Bodot.

- Among the nests classified as 'dilapidated', data collected on inhabitants and the internal state of the nest allow two categories to be distinguished: (a) nests that contained an abundant population and probably corresponded to the senile stage described by Bodot, and (b) nests in which quite a significant amount of the volume was taken up with cells that were blocked with earth but still contained functional cells with a small population and a low proportion of larvae. These nests could be described as being 'senile, in a terminal phase.'
- The nests classified as 'recent' corresponded to societies that expanded their nests during the four months preceding the survey. Indeed, the expansions made from December to March (dry season) were little affected by erosion. These nests thus probably contained growing societies and must be associated partly with juvenile societies and partly with adult societies.
- The nests classified as 'eroded' corresponded to societies that had engaged in no new con-

Table 2. Distribution of the termite mounds of Bondoé according to their apparent age and according to Bodot's age categories.

Bodot's age categories:	Young (<10 000 individuals)	Adult (10 000–40 000 individuals)	Senile (>40 000 individuals)	
Categories in this study:	Volume: <3.1 dm ³	Volume: 3.1–32.5 dm ³	Volume: >32.5 dm ³	Total (percentage)
<i>C. sankurensis</i>				
Recent	9	18	0	27 (9.2)
Eroded	10	137	50	197 (67.0)
Dilapidated	6	45	19	70 (23.8)
Total (percentage)	25 (8.5)	200 (68.0)	69 (23.5)	294 (100)
<i>C. ugandensis</i>				
Recent	3	3	1	7 (8.6)
Eroded	1	33	15	49 (60.5)
Dilapidated	0	11	14	25 (30.9)
Total (percentage)	4 (5.0)	47 (58.0)	30 (37.0)	81 (100)

struction for at least four months. They very likely hosted societies in a static condition or in a state of slow growth. They must be associated with mainly adult societies and to a lesser degree to juvenile or senile societies.

Assuming that the populations corresponding to the periods defined by Bodot (1969) for *C. severus* are applicable to the *Cubitermes* of Bondoé and using the relationship between the population of the nest and its epigeic volume established for *C. sankurensis* by Josens & Soki (2010), based on the data of Bouillon & Lekie (1964), young termite mound sizes should be lower than 3.1 dm³ and senile nests over 32.5 dm³, which enables us to construct Table 2, with the columns based on the volume of the nests.

According to this table, at the time of the survey (at the beginning of the rainy season), young societies were in the minority (5–8.5%), adult societies were in the majority (58 to 68%), and senile societies represented a significant percentage (23.5 to 37%). By reviewing Table 2, it appears (a) that nests that we classified as 'recent' correspond well to the 'young' or 'adult' nests of Bodot (only one 'recent' nest is an exception, with a size corresponding to a 'senile' nest); (b) that nests that we classified as 'eroded' are found in Bodot's three categories, and (c) the nests that we called 'dilapidated' have the size of some nests corresponding to Bodot's 'adult' and 'senile' societies; there are even six dilapidated nests that would be ranked among the 'young' nests in terms of size.

Bouillon & Lekie (1964) found that the relative

useable volume in the nests of *C. sankurensis* decreased with size (age) of termite mounds because of the thickening of inner walls. We can confirm this observation. In the fresh parts of the termite mounds the thickness of the internal walls was close to 1.5 mm at the thinnest places in *C. sankurensis* and close to 2 mm with *C. ugandensis* (measurements taken from photographs). It might therefore be possible to identify the builder according to the thickness of the walls of the nest, at least for the fresh parts since the walls are thickened later, blurring the difference between the two species.

Shape and dynamics of termite mounds

The *Cubitermes* termite mound begins as a small dome or a small cylinder with no cap. The absence of a cap generally indicates a society in which the number of individuals is still small. According to Han & Lepage (1991), with *C. fungifaber* the construction of the first cap occurs only when the total number in the society approaches 10 000 individuals. In our study, however, (a) the majority of nests without caps were dilapidated nests which had a fairly large diameter and had actually lost their caps through erosion, and (b) the construction of the first cap seemed to occur very soon. The 25 smaller nests encountered (21 of *C. sankurensis* and four of *C. ugandensis*) all had a cap or sometimes even two. Bouillon & Lekie (1964) describe no nests of *C. sankurensis* without caps and reported that only 6% of nests had two caps, whereas in Bondoé, 30% of nests had two caps and

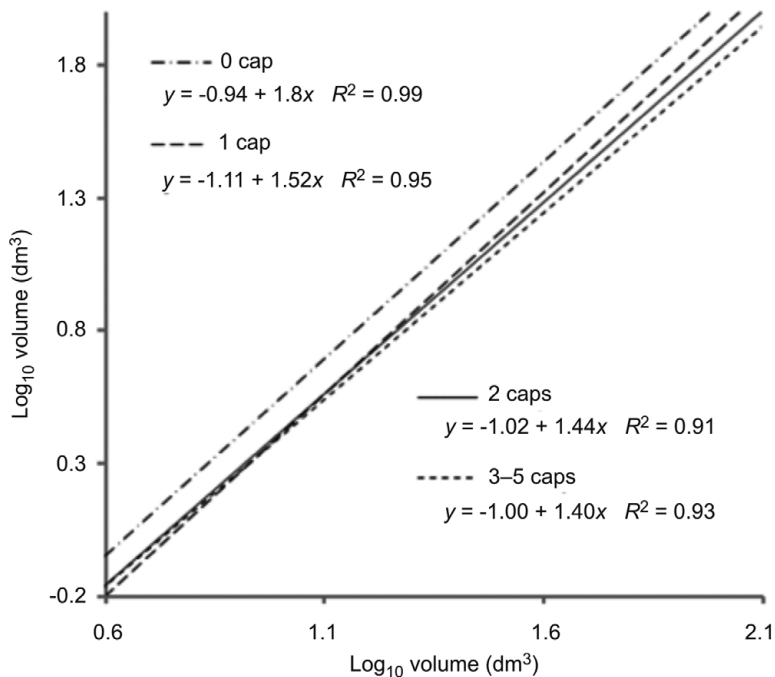


Fig. 10. Regression between the volume and surface of nests of four species of *Cubitermes*. Data from: *C. fungifaber* (Han & Lepage 1991), *C. speciosus* (Soki & Josens 1996) and *C. sankurensis* and *C. ugandensis* (this study).

6% had three or more, suggesting an older average population (unless these characteristics are related to site conditions and local climate and nutrition). In comparison with the work of Han and Lepage, we must remember that our surveys (a) were made just after the dry season, a period which is not conducive to the emergence of new nests, and (b) they were made in a savanna region, where the nests are more exposed to erosion. Indeed, Aloni & Soyer (1977) showed that the degradation of *Cubitermes* nests in Katanga is mainly due to rain erosion, which is lower in the forest where much of the precipitation is intercepted by foliage and reaches the ground via the stem flow.

A first cap would therefore play a role primarily as a shelter against rain and erosion (Emerson 1938, 1956) and the subsequent caps, would mainly allow the volume of the termite mound to be increased, and above all, increase the volume of the termite mounds while retaining the caps' protective role, which is not only to prevent erosion of the side walls but also and perhaps most important, to prevent the side walls of the nest becoming soaked by rain, thereby reducing their permeability to respiratory gases (Josens 1983).

Han & Lepage (1991) hypothesized that the addition of a cap could increase the gas exchange

surface, and it is obvious that adding a cap to a cylinder increases the total area of the nest but this must be considered in relation to the volume. In our study, nests without caps actually had a smaller surface area, at equal volume, than nests with caps. However, the regression lines (of the volume based on the surface) of nests with 1, 2 or 3 caps did not differ significantly (Fig. 8). Therefore, the addition of a second or third cap did not increase the surface area of the nest in relation to its volume.

There are four species of *Cubitermes* for which quantitative data on the volume and surface nests are available. In each case, the correlation between these two parameters is very strong and highly significant (Fig. 10) and we have already seen that the regression lines of *C. sankurensis* and *C. ugandensis* (this study) are not different. The line of *C. fungifaber* (Han & Lepage 1991) differs from the previous two only by the intercept point (*t*-test, $P < 0.01$), which means that at equal volume, the nests of *C. fungifaber* have a larger surface area (Fig. 10). This is related to their small diameter; they appear as slender columns in comparison with the more massive nests of other species. In the case of *C. speciosus* (Soki & Josens 1996) the slope is significantly (but only slightly) different

from other species (t -test, $P < 0.05$).

The water dynamics seems to have a decisive influence on the density and shape of the termite mounds. The *Cubitermes* nests are very abundant in the 'valley' southwest of the road (blocks B1 and B2). They are also present in the shrublands, on both sides of the 'valley', but with a much lower density. The termite mounds are also abundant to the northeast of the road in the block B3, but the greater the distance from the road, the scarcer they become and after a few hundred metres, they are entirely absent in a grassy area that can remain flooded for a long time in the rainy season.

The high density of *Cubitermes* nests in savanna grassland, compared with their relatively low density in the surrounding shrublands, is difficult to understand if one does not take into account niche parameters. The affinity of *Cubitermes* for shallow soils on a lateritic crust has already been reported by Maldaque (2003) and could be influenced, as suggested by Benzie (1986) by the quality of organic matter in the soil or the impact of predators. Both of these parameters depend on soil and topographic conditions. The soil of our plots is shallow, is located on a lateritic crust (outcropping in places), and is in a slight depression. In the rainy season, the soil is waterlogged and even submerged in water. These conditions probably affect the quality of humus on which the *Cubitermes* feed. They are obviously not ideal conditions for the establishment of *Cubitermes*, but we hypothesize that these conditions are even more detrimental to predators such as Doryline ants, reputed to be predatory mainly towards *Macrotermes* (Lepage & Darlington 2000) but also towards *Cubitermes* (Williams 1959; Bodot 1967). They probably avoid digging in soil that may at any time become waterlogged, so the termites may find refuge in the epigeal part of their nest. Williams (1966) reported that an association between *C. ugandensis* and *C. testaceus* is often found on the edges of wetlands, and *C. sankurensis* can be found in different types of savanna including seasonal wetlands. Nevertheless, this refuge capacity has a limit; to the northeast of the road, beyond block B3, termite mounds become scarcer, and are totally absent in an area that can be extensively flooded.

It was shown that the mounds were statistically taller, with a smaller diameter (thus slender) and with more caps in blocks B1 and B3 than in block B2, despite the fact that there were proportionally more *C. ugandensis* nests and fewer

C. sankurensis nests in Block B2 than in the other blocks (and that the mounds of *C. ugandensis* are statistically taller and larger and have more caps). This sounds somewhat contradictory. However, knowing that block B2 is the less prone to temporary flooding, and admitting that *C. ugandensis* prefers a little less wet soils, it all points to the fact that the local conditions prevail over the species in shaping the mounds. More caps mean that the termites were possibly more often stimulated to add new parts to their mounds and so build taller mounds in situations where flooding occurs more often.

The supposedly weak impact of predators in grassy savanna is supported (a) by the high proportion of dilapidated nests, with many cells filled with earth but still containing a small number of inhabitants, suggesting that many societies dwindle and then die of old age (if the nests are invaded by predators, the termites do not have time to fill the cells of their nest), and (b) the low density of *Cubitermes* nests in the nearby shrublands, in which predators potentially find more favourable conditions. If predators have little influence in the grassland it is probably intra-specific competition (for food resources) that regulates populations. And this is reflected by the fact that there are dilapidated (but not abandoned) termite mounds in all size classes, suggesting that societies can decline at any age, as a result of competition and the high density of nests.

CONCLUSIONS

The study of the shape of two sympatric species of *Cubitermes* nests in the savanna grasslands of Bongoé strongly suggests that the environmental conditions, in particular the water regime, are more influential than the species in shaping the mounds. However, the mounds of *C. ugandensis* are significantly larger than those of *C. sankurensis*.

The local conditions (temporary flooding), possibly disadvantage predators and allow the establishment of a high density of termite mounds (1297 active nests/ha) with a high life expectancy. The new mounds (societies at a young stage) emerge during the rainy season and are given a cap during their first year. Depending on the competition, especially of the intra-specific kind (very likely the two species have different diets) new societies will either collapse and die or develop (adult stage society) and the nest is enlarged by adding additional caps. As predation pressure is relatively unimportant, these nests will

last until the society reaches its maximum size (senile stage society) and will then decrease. Some parts of nests which are no longer occupied are then partially filled with earth, and the surfaces exposed to rain are eroded without being repaired, while the population size continues to decrease (senile stage society, terminal phase). The nest eventually disintegrates as a result of erosion, despite the presence of quite a large number of secondary occupants.

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