

## Research article

# Growth and demography of *Cubitermes speciosus* mounds (Isoptera, Termitidae)

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**Key words:** *Cubitermes speciosus*, Isoptera, Termitidae, mound demography, mound growth.

## Abstract

The growth and demography of *Cubitermes speciosus* mounds were studied in an equatorial forest ecosystem near Kisangani, Zaïre. The mounds were censused and measured on eight occasions from June 1985 to January 1993 on 25 plots of 100 m<sup>2</sup>.

Mounds were found to grow in two ways: either they were enlarged sporadically, leading to a correlation between age and size; or they were no longer enlarged after a 2-year period of initial growth, which means that both large and small mounds can be old.

The number of living mounds was fairly constant: it varied between 112 and 152 ha<sup>-1</sup> with an average of 139 ha<sup>-1</sup>, and about a quarter of them were renewed each year. However, a clear tendency was observed over our 7.5-year observation period: the average size of the mounds increased regularly and was 2.7 times larger in 1993 than in 1985.

Monthly birth and death rates were estimated using a model of continuous growth. Life expectancy at the age of 3 months was estimated from a survivorship curve at 3.5 years.

## Introduction

Studies on termite mound growth are still rare, and on termite population dynamics almost non-existent. In Ivory Coast, Bodot (1967) described young, mature and senile nests of *Cubitermes severus* according to their termite population content. She also described seasonal variations in building activities in relation to the climate and alate production, and noted that some mounds may stay at the same size for at least 3 years. Others addressed this question through transversal studies: Aloni and Soyer (1987) on a *Cubitermes* species in Zaïre, Benzie (1985) on *C. curtatus* and *Trinervitermes geminatus* in Ghana, Han and Lepage (1991) on *C. fungifaber* in Ivory Coast. Such transversal studies attempted to describe mound growth using mound size, termite population composition or queen size as clues for estimating the age of a colony.

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In this paper, we present the results from a longitudinal study of the population dynamics of *C. speciosus* mounds, as part of a study of an equatorial forest ecosystem. The same mound population was followed during a long period of time, which allowed us to estimate demographic parameters. To our knowledge, such a demographic study on termite nests had never before been attempted.

### Study site

This work was carried out in the Masako Reserve (0°31'N, 25°11'E), located 14 km north of Kisangani, Zaïre, in a primary *Gilbertiodendron dewevrei* forest. The soil is ferralitic and of a sandy-clayed texture. The climate is of the equatorial type with an average annual rainfall of about 1800 mm. The mean monthly temperature fluctuates in a narrow range: 22.5–26 °C. Relative humidity is generally above 80%. Rainfall is normally highest in October. A regular dry season occurs in January and early February, and a lesser dry period may take place in July or August. According to the Zaïrian Meteorological Service, this climate pattern was followed in 1988 and 1989. In 1990, however, there was no lesser dry season and October rainfall was less abundant than expected.

### Material and methods

#### *Mound sampling*

An area of 4 ha was delimited and subdivided into 10×10 m squares. 25 of these squares were chosen randomly and sampled repeatedly. Each *C. speciosus* mound was measured, drawn, cored superficially, located on a map and painted with a white diluted (10%) latex paint. Coring the mounds (about 1 cm in diameter) was done to check if societies were still alive and painting enabled us to recognize if the mounds had been enlarged on subsequent samplings. Samplings were performed in June 1985, January 1987, June 1987, October 1988, March 1989, December 1989, March 1991 and January 1993. A partial sampling was performed in June 1986.

The approximative volume of the epigeic part of a nest was estimated assuming that the mound was a cylinder the height of which was the measured mound height. If the mound had no cap, its diameter was calculated from the perimeter at mid-height, if one or more caps were present, its diameter was calculated from the perimeter just underneath the first cap.

#### *Demographic parameters*

Since the mounds of *C. speciosus* are long-lived and their birth (emergence) and death occur continuously, we used the classical continuous mathematical model for describing their demography (Pielou, 1977; Vandermeer, 1981):

$$\frac{dN}{dt} = \beta N - \delta N = rN \quad (1)$$

where  $N$  = number of mounds

$\beta$  = instantaneous birth rate

$\delta$  = instantaneous death rate

$r$  = intrinsic rate of natural increase (instantaneous net growth rate)

These demographic parameters were estimated as follows. If all the mounds are marked at  $t=0$ , then the number of surviving mounds ( $S$ ) follows the equation:

$$\frac{dS}{dt} = -\delta S \quad \text{with } S_0 = N_0$$

Hence  $S = N_0 e^{-\delta t}$

$$\text{and } \delta = \frac{1}{t} \ln \frac{N_0}{S} \quad (2)$$

The instantaneous net growth rate  $r$  can be computed directly from equation (1):

$$r = \frac{1}{t} \ln \frac{N}{N_0} \quad (3)$$

Finally:

$$\beta = r + \delta = \frac{1}{t} \ln \frac{N}{S} \quad (4)$$

In this study, letting:

$i$  = sampling number,

$t_i$  = date of sampling  $i$ ,

$\Delta t_i$  = time lapse between samplings  $i-1$  and  $i$ ,

$N_i$  = number of living mounds at  $t_i$ ,

$B_i$  = number of new mounds at  $t_i$ ,

$D_i$  = number of mounds that were living at  $t_{i-1}$  and dead at  $t_i$ ,

equations (2), (3) and (4) become, respectively:

$$\delta_i = \frac{1}{\Delta t_i} \ln \frac{N_{i-1}}{N_{i-1} - D_i} \quad (5)$$

$$r_i = \frac{1}{\Delta t_i} \ln \frac{N_i}{N_{i-1}} \quad (6)$$

$$\beta_i = \frac{1}{\Delta t_i} \ln \frac{N_i}{N_{i-1} - D_i} \quad (7)$$

The life expectancy of a mound at age  $x$  was estimated from the survivorship curve using the following equation, which is a modified form of the standard formula (Vandermeer, 1981):

$$e_x = \frac{1}{S_x} \sum_{i=x}^{i=x \max} \left( \frac{S_i + S_{i+1}}{2} \right) \Delta t_i \quad (8)$$

where  $e_x$  = life expectancy at age  $x$ ,

$S_x$  = estimated number of surviving mounds at age  $x$ .

## Results

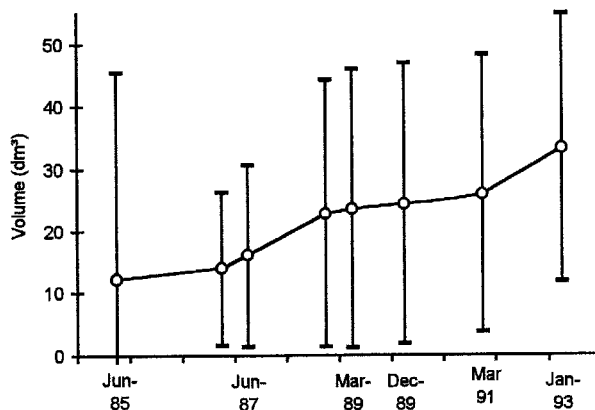
The raw data for the successive samplings are given in Table 1.

### *Mound size distribution*

Quite unexpectedly, mean mound size increased continuously from June 1985 (12.2 dm<sup>3</sup>) to January 1993 (33.3 dm<sup>3</sup>) (Fig. 1). Despite large variances, these means differed significantly (Student-Newman-Keuls test,  $p < 0.05$ ). Size distributions also differed significantly ( $\chi^2 = 31.3$ , 4 df,  $p < 0.001$ ): in June 1985, a large majority (76%) of the mounds were less than 10 dm<sup>3</sup>, whereas in January 1993 such small mounds accounted for only 9% (Fig. 2). Intermediate samplings exhibited intermediate size distributions.

### *Individual mound growth*

Very small mounds are narrow columns that grow in both diameter and height. The first cap is built when the height reaches about 40–45 cm. Subsequently, additional caps may be constructed but the diameter at the base, in most cases, no longer



**Figure 1.** Changes in living mound size of *Cubitermes speciosus* (mean volume  $\pm$  standard deviation) over the 7.5-year observation period

**Table 1.** Volumes (in dm<sup>3</sup>) of *Cubitermes speciosus* living mounds on the 2500 m<sup>2</sup> sampling area

Mound #	June 85	Jan 87	June 87	Oct 88	Mar 89	Dec 89	Mar 91	Jan 93
1	6.4	19.0	32.2	32.2	43.7	43.7		
2	10.1	12.2	13.5	20.4	21.8	21.8	21.8	
3	0.85	6.7	12.5	14.1	18.7	18.7		
4	0.63							
5	5.9	16.1	16.1	16.1	16.1	16.1		
6	2.1	4.7						
7	7.5							
8	8.4	10.3	17.7	17.7	24.7	24.7		
9	0.52							
10	0.29							
11	11.4	33.8	33.8	33.8	33.8	33.8	33.8	
12	2.5	6.5						
13	9.3	40.0	41.9	52.8	60.3	60.3		
14	0.40							
15	30.2	30.2	42.2	42.2	42.2	42.2	42.2	42.2
16	27.2	28.9	28.9	28.9	28.9	28.9	28.9	
17	7.4	15.9	20.5					
18	0.04							
19	8.2	16.6	16.6					
20	0.89	8.1						
21	6.0							
22	32.1	54.2	54.2	54.2	54.2	54.2	54.2	54.2
23	18.8	21.4	21.4					
24	205.7							
25	0.13							
26	12.2							
27	2.8	15.4						
28	1.69							
29	16.4	25.6	25.6	25.6	47.2	47.2	49.8	49.8
30	3.7	20.6	20.6	20.6	26.2	26.2	49.2	49.2
31	0.67	3.3	9.3	18.5	18.5	18.5	18.5	
32	0.60							
33	1.37	7.1	7.1	15.5	15.5	15.5		
34	5.2	22.7	24.8	24.8	24.8	24.8	24.8	24.8
35	0.38	2.2						
36	7.1							
37	7.3	15.5	16.3	16.3	16.3			
38	2.8	29.5	47.2	51.2	51.2	51.2	51.2	51.2
39		1.38	3.6	20.2	22.5	25.0	25.0	59.9
40		0.20	5.3					
41		0.48	2.8					
42		4.1	8.0	10.5	16.3	16.3	16.3	16.3
43		3.8	4.1	6.6	6.6			
44		8.0	8.0	11.8	11.8	11.8	11.8	
45		14.5						
46		6.1						
47		10.3	10.3	16.2				
48		0.23	1.80	6.2	11.2	11.2	11.2	38.6
49		6.3						
50		1.6	2.4	8.4	8.4	17.0	17.0	
51		1.2	3.0	4.1	17.2			

**Table 1** (continued)

Mound #	June 85	Jan 87	June 87	Oct 88	Mar 89	Dec 89	Mar 91	Jan 93
52			1.43	4.3	4.3			
53			3.7					
54			0.83	1.38	1.38			
55			1.24	11.4				
56			4.8	4.8	5.6	5.6	8.6	26.1
57				0.36				
58				105.3	105.3	105.3	105.3	105.3
59				44.5	44.5	44.5	44.5	44.5
60				6.5	19.9	19.9	19.9	19.9
61				51.7	51.7	51.7		
62				0.14				
63					0.08	0.34		
64					0.19			
65					0.70	2.1	11.4	
66					0.10	0.63		
67					0.09	0.66		
68					0.24			
69						1.97		
70						2.8	2.8	
71						0.60		
72						29.1	29.1	29.1
73						0.57	17.8	46.4
74						3.0		
75							5.1	
76							15.9	34.3
77							1.05	
78							2.2	34.9
79							7.6	28.1
80								16.5
81								17.7
82								30.1
83								21.0
84								4.6
85								25.2
86								6.0
87								71.8
88								41.4
89								10.1
90								15.4
91								36.7
92								3.3
93								10.1
Aver. volume	12.24	13.96	16.10	22.83	23.57	24.38	25.96	33.26
± std dev.	±33.26	±12.33	±14.51	±21.47	±22.37	±22.52	±22.28	±21.55
Number of mounds	38	38	35	35	37	36	28	32

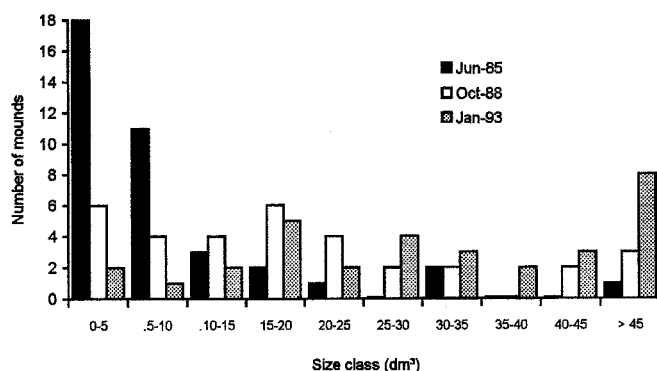


Figure 2. Frequency distributions of mound sizes of *Cubitermes speciosus* in June 85, October 88 and January 93

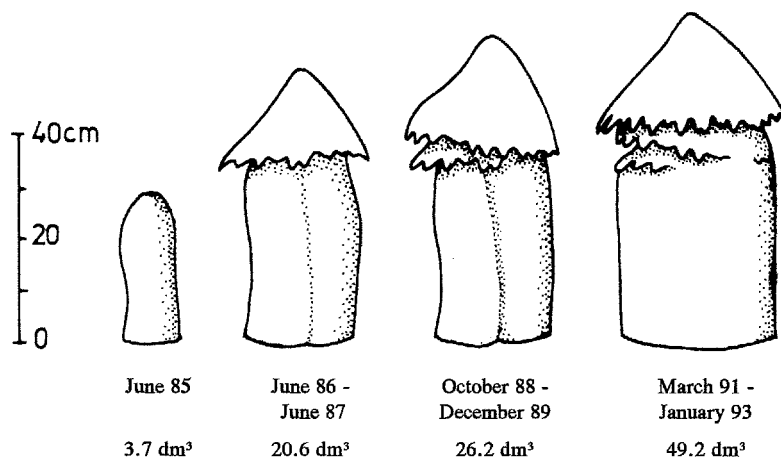


Figure 3. Growth of mound # 30, following the discontinuous growth pattern. The late enlargement of the mound base (between December 1989 and March 1991) was rarely observed

increases. In some other cases, however, either a second and a third column can be appended to the initial mound or the initial base can be enlarged (Fig. 3).

The increase of the mound volume followed two patterns that were described from a batch of 49 mounds encountered when they were small ( $< 20 \text{ dm}^3$ ) in June 1985, January 1987 or June 1987 and that lived for at least 5 years. A majority of mounds grew during one or two years and stayed subsequently alive without any further increase (Fig. 4). 32 of the 49 mounds followed this “upper limited growth pattern”. A minority of mounds grew with one or two intermediate plateaus (Fig. 5); they did not grow continuously. 17 of the 49 mounds followed this “discontinuous growth pattern”.

Individual mound growth rates were high during periods  $\Delta t_2$ ,  $\Delta t_3$ ,  $\Delta t_4$  and  $\Delta t_7$ , and low during periods  $\Delta t_5$  and  $\Delta t_6$  (Table 2). Some indices of seasonality can be

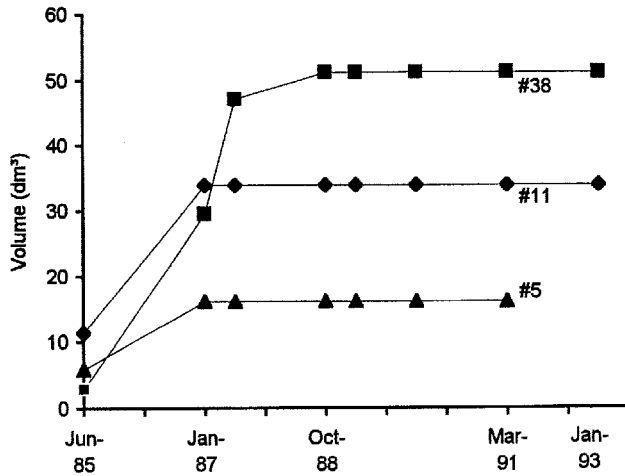


Figure 4. Three examples of the upper limited growth pattern (mounds # 5, 11 and 38)

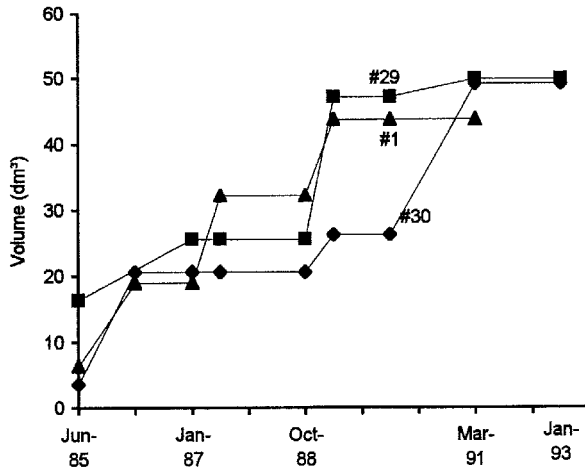


Figure 5. Three examples of the discontinuous growth pattern (mounds # 1, 29 and 30)

deduced from the comparison of short intersampling periods.  $\Delta t_3$  was significantly lower than  $\Delta t_2$  ( $p=0.022$ ) and  $\Delta t_4$  ( $p=0.046$ ), suggesting a faster growth during the first half of the year. Sporadic field observations located the main building activities during January, February and March, during and following the dry season.

*Mound demography*

The number of mounds on the 2500 m<sup>2</sup> sampling area was roughly constant: it varied between 32 and 38 in all censuses but one. Only in March 1991 did this number drop to 28 mounds (Table 2). Thus the average density was 139 mounds/ha.



**Table 2.** Demographic parameters of the mound population and individual mound growth rates on the 2500 m<sup>2</sup> sampling area

Sampling number	Date (t)	$\Delta t$ months	Number of mounds	$g$	$B$	$D$	$\beta$	$\delta$	$r$
0	06/85	–	38	–	–	–	–	–	–
1	01/87	19	38	$0.43 \pm 0.40$	13	13	0.022	0.022	0
2	06/87	5	35	$0.55 \pm 0.83$	5	8	0.031	0.047	-0.016
3	10/88	16	35	$0.55 \pm 1.27$	6	7	0.014	0.014	0
4	03/89	5	36	$0.55 \pm 1.00$	6	5	0.037	0.031	0.006
5	12/89	9	37	$0.16 \pm 0.55$	6	6	0.020	0.020	0
6	03/91	15	28	$0.21 \pm 0.41$	5	13	0.013	0.030	-0.017
7	01/93	22	32	$0.70 \pm 0.76$	14	10	0.026	0.020	0.006
Total		91			55	62	0.021	0.023	-0.002
Correlation coefficient $\rho$				$g-\beta: \rho=0.77, p<0.05$		$\beta-\delta: \rho=0.55, n.s.$			
				$g-\delta: \rho=0.51, n.s.$					

$g$  = individual mound growth rate (dm<sup>3</sup>/month, average  $\pm$  standard deviation)

$B$  = Number of newly emerged mounds

$D$  = Number of mounds that have died since the previous sampling

$\beta, \delta$  and  $r$  = instantaneous birth, death and net growth rates (month<sup>-1</sup>) of the mound population

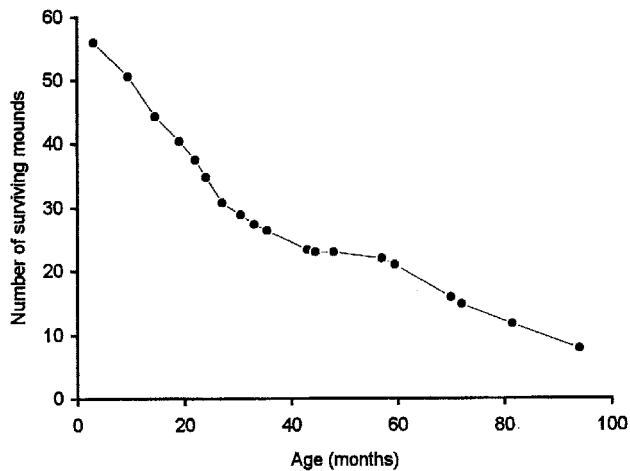
The demographic data and estimated parameters are summarized in Table 2. In all cases the death rate was balanced by the birth rate or almost so. Only during periods  $\Delta t_2$  and  $\Delta t_6$  did the death rate exceed the birth rate, resulting in a slightly negative net growth rate. The overall net growth rate was almost zero.

To build an approximate survivorship curve for the mound population (Fig. 6), we used an initial population of 55 mounds made of: (1) 37 out of the 38 mounds recorded in June 1985 (only the very large mound no. 24 was discarded); given their small size, it was assumed that at least 75% of them had emerged during the 6 preceding months; therefore they were assigned a mean age of 3 months; (2) the 13 mounds first recorded in January 1987; these were given a mean age of 9.5 months (half of the time period since the previous census); (3) the 5 mounds first recorded in June 1987; these were given a mean age of 2.5 months (half of the time period since the previous census).

Six out of the 37 mounds marked in June 1985 (and not the smallest ones) were still alive in January 1993 and were therefore more than 7.5 years old. Mortality was found to be more or less constant over a period of 7 years. The survivorship curve could therefore be interpolated, which enabled calculation of life expectancies (Table 3). Life expectancy at the age of 3 months was estimated at 3.5 years.

#### Settlement success rate

In 1989, 1990 and 1991, the production of alates accounted for  $5.1 \pm 1.6$  (s.d.)% of the termite population in the mounds (Soki, 1994). It was therefore estimated that about 380,000 alates must have swarmed on the 2500 m<sup>2</sup> surveyed area between



**Figure 6.** Survivorship curve of *C. speciosus* mounds constructed from a batch of 55 mounds first recorded on the 2500 m<sup>2</sup> sampling area in June 1985 (37 mounds), January 1987 (13 mounds) or June 1987 (5 mounds)

**Table 3.** Life expectancy of *C. speciosus* mounds (in years)

Age $x$	0.25	1	2	3	4	5	6	7
Life expectancy at age $x$	3.45	3.49	3.51	3.55	3.00	2.25	1.96	1.40

June 1985 and January 1993, that is, 190,000 potential pairs or settlements. During the same period 55 new mounds emerged, which gives a success rate of 0.029% only.

## Discussion

### *Correlations between parameters*

Birth and death rates were not significantly correlated (Table 2). Such a correlation was not expected and, in fact, if there is strong intraspecific competition, a delayed correlation would be more logical since swarms occur only once a year in April–May (Soki, 1994) and newly settled societies are not expected to build epigeic nests until they reach a minimum size.

A significant correlation was found between mound population birth rate ( $\beta$ ) and individual mound growth rate ( $g$ ), suggesting that building activities either for enlarging the mounds or making new ones occur simultaneously, mainly from January to March. Under savanna climatic conditions, building activities were regularly reported to occur at the beginning of or during the rainy season, when the soil is wet and favourable for this activity (Bodot, 1967; Darlington, 1983, 1986; Aloni

and Soyer, 1987). In the primary forest, *C. speciosus* building activity does not seem to be seasonally limited but the relative dry season might be most favourable.

#### *Reliability of birth and death rates*

Birth and death rates may have been both under- and overestimated. On the one hand  $\beta_i$  and  $\delta_i$  were probably underestimated because the time lapse between subsequent samplings varied between 5 and 22 months. New mounds may have emerged and died between two sampling dates without having been censused. On the other hand some of the newly emerged mounds were produced probably by moving colonies. In this case, assuming that an old mound is abandoned to build a new one, both birth and death rates would have been overestimated. Thus our estimates of demography rates should be viewed as approximate rather than precise values and should concern mounds rather than colonies.

Nest moving seems to be rare in *C. speciosus* when mounds are small but might become more frequent in medium-sized and large colonies as it was found in *C. fungifaber* (Han and Lepage, 1991). Nine out of the 55 mounds that emerged after June 85 had a large volume ( $> 25 \text{ dm}^3$ ) when first censused and those that were first encountered in October 88 (mounds 58, 59 and 61) stayed at the same size until January 93, suggesting that those societies moved when they were almost mature, maybe in response to an increasing local competition with neighbouring colonies.

#### *Population stability and long-term changes*

The number of inhabited mounds was fairly constant during the 7.5 years of this study. The only significant drop was noticed in March 1991 and resulted from both a low birth rate and a rather high death rate during period  $\Delta t_6$ . This may have been a consequence of the 1990 weather conditions, the seasonal variations of which were less strongly marked than normally. It is worthwhile to mention that during the subsequent  $\Delta t_7$ , the birth rate was rather high and the death rate rather low, suggesting that a recovery of the population was taking place.

While the mound population was stable, the mean mound size increased regularly over the 7.5-year observation period. Using a regression between the number of termites and the mound volume (Soki, 1994), it was estimated that the overall termite population in the mounds increased from 2.5 to 5.6 million individuals/ha. This regular increase strongly suggests that this population was not limited by intraspecific competition in the beginning of our study period. Such a long-term trend has never been described before and would be worth studying over a longer time period.

We cannot exclude that this trend is part of a long-term population oscillation. However, no change was observed in either vegetation or human impact in the forest of the Masako Reserve. The fact that a majority of very small nests were found in June 1985 gives the impression that the population at that time was recovering from a dramatic mortality. And since these small nests were found on 25 plots of  $100 \text{ m}^2$  spread on an area of 4 ha, an epidemic seems to explain such a mortality

better than does a predator. Nest ageing during population recovery would then at least partly explain the observed tendency towards an increasing mound size.

A similar impression arises from a set of observations performed in the Mayombe forest, Congo Republic, on a population of *Thoracotermes macrothorax* mounds (Rouland, personal communication). On an area of 5 ha, about 75 colonies (almost all the nests of this species) died between July 86 and March 87. The remaining mounds had not been destroyed but were crumbly. The other mound-building species (*Noditermes* sp. and *Cubitermes* sp.) had not been affected. During the subsequent years the *T. macrothorax* mound population gradually recovered. In this case also, the rapid spread of a species-specific disease or parasite seems plausible. This stresses the need for research into the role of diseases and parasites in the population dynamics of termites.

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