Estimates of food consumption by the fungus-growing termite *Macrotermes natalensis* in a South African savanna-woodland

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THIS STUDY QUANTIFIES AND DISCUSSES food consumption by the termite *Macrotermes natalensis* based on gut analysis. It introduces a formula that is used to determine the amount of food consumed by foraging organisms such as termites. The annual food consumption is given by the formula 365 *mnp/t*, where m = individual mass of ashed crop-gizzard contents, n = number of foraging major workers, p = daily foraging period, and t = individual time spent between nest and food source. The mass of food that is consumed during a single foraging trip by a foraging individual is 0.166 ± 0.009 mg. Food consumption of this termite in the northern Kruger National Park is estimated to be on average 20.2 kg ha^{-1} yr^{-1}. The quantification of food consumption by this termite makes possible an assessment of its role in nutrient cycling.

The ecological importance of macrotermitine termites in nutrient cycling is augmented by their high consumption per unit biomass, which is facilitated by nitrogen-rich fungal symbiosis.[1,2] The midgut (mesenteron) is a major site of cellulose breakdown, which is accomplished using enzymes that are acquired by the Macrotermitinae through ingestion of fungal nodules or synemata (mycophagy) rich in these enzymes.[3] Mainly old major workers collect forage (litter) outside the nest.[4,5]

Workers of *Macrotermes natalensis* (Haviland) (Isoptera: Termitidae) venture outside the mound in underground passages, exiting the soil surface near or at the food source, such as fallen branches or twigs. Evidence of foraging is left in the form of a thin sheet of soil constructed over the food source. Sometimes the termites surface before they reach the litter and construct covered runways (Meyer, pers. obs.).[6] Soldiers are fed by the workers and do not forage directly; the protection that they offer to foraging workers is a cost of foraging.[5,7]

Food is ingested into the crop and gizzard of the foraging termite workers and transported to the nest, where it is regurgitated for distribution and digestion.[8,9] Stomodeal food in the foregut of foraging workers represents the amount of litter removed by their foraging effort.

Because of the cryptic foraging behaviour of this species (Meyer, pers. obs.),[10] estimation of removal of litter (mainly wood) was explored using analysis of gut contents.

Sampling and gut analysis

Foraging termites (major workers) were collected from beneath soil sheeting at natural food sources (woody litter) present at different distances around mounds. Woody litter was gently lifted and exit holes were immediately blocked to prevent fed foragers from departing and unfed foragers from arriving. Major workers were carefully picked up by the head and placed in Petri dishes with forceps (standard collection technique). They numbered approximately 2000 in total.

The major workers collected were promptly taken to the laboratory, where their gut contents were removed. This was done by applying pressure around the thorax and abdomen, thereby forcing the contents through the anus. Care was taken not to remove the trophic membranes. The samples (gut contents) were dried for 48 h at 70°C and weighed in the closed chamber of a microbalance to the nearest 0.0001 g. The mass of dry gut contents was obtained by dividing the mass of each of the ten samples by the number of individuals (*c.* 200) present in each sample. Dried samples were ashed in a bomb calorimeter or a muffle furnace (4 h at 600°C) and subsequently reweighed in order to determine the amount of organic material present in the gut samples. Both combustion and incineration gave similar ashing results. The ash mainly represents soil particles such as sand and quartz contained in the digestive tract of these workers.

The fraction of gut contents present in the crop and gizzard was determined using standard volume formulae for the different sections of the uncoiled digestive tract in major workers that foraged.[11]

Foraging frequency

The frequency of visits to the food source from the mound and back was observed through a translucent Perspex tube (1 m × 40 mm) during different times of the day and night across seasons. The tube was laid horizontally as a passage directly between the mound and food source,[7] and covered with soil when observations were not being made. Observation was hampered by condensation inside the tube. Termites were reluctant to make use of tubes longer than a metre.

Determination of annual food consumption

The mass of inorganic components in the gut contents was subtracted from the dry mass of the gut contents. Since freshly foraged material present in the crop and gizzard represents the amount of litter consumed, obtaining the dry mass of this material allows one to measure biomass consumed. Foraging frequency was expressed as daily foraging period (timespan of foraging activity in 24-h day) divided by individual foraging time, that is, number of return trips. The annual estimate of food consumed by these termites is given as 365 *mnp/t*, where m = individual ash-free mass of gut contents in crop-gizzard, n = number of foraging major workers, p = daily foraging period, and t = individual time spent between nest and food source.

Unless otherwise stated, means are given with their 95% confidence intervals using the standard error and two-tailed t distribution. As consumption per unit area is a linear projection of mound density,[12] annual food consumption is reported as an overall mean based on density.

Findings and conclusion

Minor workers made up a small percentage of foraging workers, but did not participate in foraging. Soldiers were ignored and not collected, as they do not forage for litter.

Dry mass of the gut contents in a major worker was determined to be 1.483 ± 0.145 mg (n = 10), of which 42.4 ± 2.3% (n = 5) is ash. The proportion of food directly consumed by a foraging individ-

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ual (stored in crop-gizzard) is 19.5 ± 2.1% (n = 10) of the ash-free material in the total gut. The mass of the food consumed by a foraging individual is 0.166 ± 0.009 mg.

The number of major workers foraging from small, medium and large colonies was estimated from previous studies to be 1117 ± 720 (n = 3), 7310 ± 672 (n = 16) and 45 329 ± 12 014 (n = 16), representing 35.5% of all workers in these colonies (Meyer, unpubl.).[13]

The foraging period comprises approximately 12 h (43 200 s) of a 24-h day, and usually takes place nocturnally (Meyer, pers. obs.).[4,6,8]

By employing the formula that we developed and using the values for all the variables mentioned, overall food consumption of *M. natalensis* in the northern Kruger National Park (KNP) is estimated to be 20.19 ± 11.45 kg ha^{-1} yr^{-1} (n = 20 landscapes) established using dry, ash-free gut (crop-gizzard) contents.

Consumption of litter was previously studied by comparing the mass of food before and after it had been fed upon.[1,14] In some studies artificial bait was used, but that approach may not reflect the true rate of natural consumption.[4,15] A common concern with regard to these studies is that the termites may not solely be responsible for litter removal. Hence the amount of litter removed by termites may be overestimated.

Collins,[16] using a baiting technique, reported consumption of *Macrotermes bellicosus* (Smeathman) in Nigeria to be 225.91 kg ha^{-1} yr^{-1}, which is an order of magnitude higher than that of the present study (20.19 kg ha^{-1} yr^{-1}). However, Collins' estimate was expressed as dry mass (including ash), whereas that of the present study excludes ash. When using the biomass of *M. natalensis* for the northern KNP (0.51 kg ha^{-1})[17] together with the consumption rate given for Nigeria (48.11 kg consumed per kg biomass per yr), we calculate consumption to be 24.53 kg ha^{-1} yr^{-1} for the study area, which is similar to our estimate in KNP. Given the different mound densities — 0.27 ha^{-1} in KNP[12] and 6.45 ha^{-1} for the Nigerian study site[16] — it is likely that this can account for the differences in food consumption reported at the different localities.

When the relationship between litter production and rainfall[18] is used to predict litter production in the northern KNP based on annual rainfall,[19] we conclude that *M. natalensis* consumes 3.4% of the woody litter produced annually compared to 4.7% consumed by *M. bellicosus*.[16] Both regions have woodlands dominated by the pod-bearing Caesalpinioideae (Fabaceae), and it appears that these two allopatric species have similar roles in decomposition in their habitats.

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Brunet delivers Broom Memorial Lecture

This year's Robert Broom Memorial Lecture was given by Michel Brunet of the University of Poitiers in France. Speaking at the Transvaal Museum in Pretoria on 13 June, Professor Brunet elaborated on hominid origins and in particular on Toumaï, 'the earliest hominid'.

From left: Michel Brunet (holding a cranium of a modern chimpanzee), Jean Cadet, Ambassador of France in South Africa (holding a cast of Toumaï), and Francis Thackeray of the Transvaal Museum (with a cast of 'Mrs Ples' from Sterkfontein), in the Broom Room of the museum, on the day of the Broom memorial lecture.

The new fossil hominid, named *Sahelanthropus tchadensis* and recovered by the Mission Paléoanthropologique Franco-Tchadienne from the Late Miocene of Toros-Menalla in northern Chad, is associated with 42 species of which the mammalian component indicates an age close to 7 million years. The find was reported in *Nature* on 11 July 2002 (**418**, 145–151) by Brunet and 37 co-authors, including Djimdoumalbaye Ahounta, a Chadian palaeontologist who discovered the fossil in the Djurab desert.

The associated fossilised animal remains include aquatic and amphibious vertebrates, together with fauna representing gallery forest, wooded savanna and grassland. The sediments support the reconstruction of a mosaic of environments between a large lake (Mega Chad) and desert, perhaps not unlike the Okavango Delta today. The Toumaï individual displays a combination of characters that suggests that it is probably close in time to the common ancestor of chimpanzees and humans.

The geographic location of Toumaï, 2500 km west of the East African Rift Valley, along with its great antiquity, suggest a widespread hominid distribution, and an earlier chimpanzee–human divergence (at least 7 million years ago) than previously indicated by some molecular studies.

Both Toumaï from Chad, and 'Mrs Ples' from the Sterkfontein Caves in South Africa, can be consided distant relatives of all humankind. In his lecture, Brunet emphasized the significance of Africa as the continent which could justifiably be called 'The Cradle of Humankind'.