Trophic interactions among invertebrates in termitaria in the African savanna: a stable isotope approach

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Abstract. 1. Termites (Isoptera) in tropical savannas are known as ecosystem engineers, affecting the spatial and temporal distribution of water, carbon, cations, and nutrients through their mound structures. Their mounds, however, also offer habitation to diverse taxa and feeding guilds of other invertebrates; a keystone role that has not been properly quantified.

2. The aim of this study was to explore the ecosystem role of termitaria in determining invertebrate diversity and their potential trophic interactions. We used stable isotopes to distinguish termite-feeding invertebrates from invertebrates merely living in termite mounds under field conditions.

3. The results suggest that inquiline spiders (Arachnida) do not feed on termites directly, but on other invertebrates within the termitaria that are termitophagous, elevating the spiders three trophic levels higher than the termites.

4. This study is the first to demonstrate food web interactions among inquiline invertebrates with a stable isotope approach. It provides evidence that termites play a keystone role in the system by providing habitat for various, trophically interacting invertebrates. These results illustrate a rather unexplored ecosystem property of savanna termites.

Key words. Arachnida, $\delta^{13}C$, $\delta^{15}N$, food web, inquiline, Serengeti National Park, termites, trophic level.

Introduction

Termite mounds, or termitaria, are conspicuous nest structures, shaped to accommodate and regulate the internal climate and the exchanges of respiratory gases between the nest and atmosphere (Lüscher, 1961; Darlington, 1984; Korb & Linsenmair, 1998). These structures, built from the surrounding subsoil, encompass a network of tunnels and ventilation shafts that create a homeostatic environment for the colony and, in case of the Macrotermitinae, for the inhabiting symbiotic fungi of the genus *Termitomyces*. In tropical savannas, termites (Isoptera) form a central component of the nutrient cycling processes. As ground dwelling decomposers they are regarded by some authors to fulfil the equivalent ecological role of earthworms in temperate regions with regard to soil conditioning (Lavelle, 1997; Brown *et al.*, 2000). Known as ecosystem engineers, termites affect the spatial and temporal distribution of water (Holt *et al.*, 1996), carbon, basic cations, and other micro-nutrients (Lobry de Bruyn & Conacher, 1990; Scholes & Walker, 1993), all of which are essential resources in arid and semi-arid ecosystems. The vegetation surrounding the mounds benefits from these accumulated resources through erosion of the mound (Coventry *et al.*, 1988). Moreover, in open savannas termite mounds and below ground cavities create a distinct feature in an apparently homogeneous landscape (Jarman & Sinclair, 1979; Belsky, 1988). The mounds provide shelter from sun and a safe home to a diverse group of mammals, reptiles, and invertebrates (Redford, 1984), termed collectively as inquilines; describing every other inhabitant of the mound including any termites that did not actually build it. In addition, the mound and its inhabitants present a central source of food, attracting several known vertebrate (e.g. Kingdon, 1977; Abensperg-Traun, 1994) and invertebrate (Sheppe, 1970) predators.

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As social insects, termites offer a source of food that is spatially patchy, but relatively permanent and of high quality (Redford, 1987). Compared with ants, an individual termite is more defenceless; termites rely mostly on the strong mandibles of the soldier caste, although some species show abdominal dehiscence (Noirot & Darlington, 2000). Furthermore, termites have softer exoskeletons than ants that make them more digestible (Redford & Dorea, 1984). Generally, termites are seen as easier targets for predators (Sheppe, 1970). So far, mainly mammals, reptiles (Kruuk & Sands, 1972; Kingdon, 1977; Abensperg-Traun, 1994), birds (Dial & Vaughan, 1987; Korb & Salewski, 2000), and ants (e.g. Sheppe, 1970) have been reported to eat termites. Other invertebrate predators have received less attention, which is surprising given the potentially large number of termitophagous invertebrate taxa reflecting the immense diversity of invertebrates occurring in the same tropical habitats as termites (Coaton & Sheasby, 1972). Relatively few publications report cases, where invertebrates other than ants act as predators of termites, and these have largely been anecdotal field studies (Sheppe, 1970; McMahan, 1982; Nentwig, 1986; Dean, 1988; Eberhard, 1991; Dippenaar-Schoeman *et al.*, 1996; Jones & Cumming, 1998; Wesolowska & Cumming, 1999, 2002).

As predator–prey interactions among invertebrates are difficult, if not impossible, to quantify in the field through direct observations, we used the natural stable isotope signature of biomass to elucidate trophic relationships among invertebrate taxa. Stable isotope technologies developed in the past decade provide alternative methods for food web analysis, which have been successfully applied in freshwater and marine systems and increasingly in terrestrial communities, especially soil communities (Ponsard & Arditi, 2000; Scheu & Falca, 2000). A series of stable isotope studies focused on termites, but these analyses were performed to study the food habits of these insects themselves (e.g. Boutton *et al.*, 1983; Spain & Reddell, 1996; Tayasu *et al.*, 1997; Tayasu, 1998). Stable isotope analysis has, to our knowledge, never been used to identify invertebrate predator–prey interactions in the field with termites acting as prey. Compared with their better-quantified role in nutrient cycling, the ecosystem role of termitaria from a trophic perspective received less attention.

In this study, we inferred potential feeding relationships between termites and other invertebrates inhabiting the same mound (not the surrounding landscape matrix) by determining the stable isotope composition of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in their body tissues. This represents a time-integrated diet of an organism in which the $\delta^{15}N$ of any given consumer is increased by ~ 3‰ compared with its diet (DeNiro & Epstein, 1981; Vanderklift & Ponsard, 2003). ^{15}N enrichment (expressed as Δ) has been used to calculate trophic positions of organisms (Hobson & Welch, 1992; Post, 2002) and the number of steps of size Δ between them as a measure of their level in the food chain or position in the food web (Hobson & Welch, 1992). The $\delta^{13}C$ changes little as it moves through the food web (Rounick & Winterbourn, 1986; Post, 2002) and therefore can be used to evaluate the carbon sources of an organism (for terrestrial systems differentiating between vegetation with C_3 and C_4 photosynthetic pathway).

The aim of this study was to reveal potential trophic interactions between termites and other inquiline invertebrates living within the same termite mound. From field inspection it was found that the ventilation chimneys of termitaria in the tropical savanna of Serengeti National Park (SNP), Tanzania, often contain spiders in high abundance. We investigated whether these inquiline spiders are potentially termitophagous or are predating on other invertebrates inhabiting the same microhabitat and in this way making use of the structure and prey diversity of the termite mounds.

Methods

Study site

This study was conducted in the Serengeti National Park (SNP), Tanzania, during the dry season (October) of 2005. SNP is located in the north of Tanzania as part of the wider Serengeti-Mara ecosystem (34° to 36°E, 1°15′ to 3°30′S). The collection sites were located in the medium height grass plain region of SNP.

Collection and preparation

Sixteen active termite mounds from different species and containing chimneys were selected throughout the study area. Termites, spiders and other ground-dwelling invertebrate taxa were collected manually with forceps from the outside of the termite mounds as well as the inside of the chimneys and stored in vials until frozen in the lab. Termites were collected by excavating a section (ca. $30 \times 30 \times 30$ cm) of the mound. Other invertebrates and spiders were collected during a search period of 10 min per mound. Invertebrates were transferred to the isotope laboratory of the Technische Universität München, Lehrstuhl für Grünlandlehre, Germany, for the remaining procedures.

Termites were identified to genus level according to Uys (2002). Before processing of the other invertebrates took place, detailed pictures were taken with a Binocular Stemi SV 11, magnification level 10 and 0.6–2.5 fine magnifier at the Lehrstuhl für Genetik, Technische Universität München. Invertebrates were identified to family level according to Picker *et al.* (2002) and with the help of specialists Steve Pilcher (Dartmoor Zoological Park, U.K.), Tony Russell-Smith and Ian Dawson (British Arachnological Society).

Stable isotope analysis

Soil-contaminated samples and webbed spiders were gently washed with demineralised water and thereafter dried at 60°C for 48 h as predetermined by pilot calibrations. The invertebrates were weighed, and then ground to homogeneity with a mortar and pestle. Samples of 0.3–0.4 mg were taken (in most cases corresponding to the entire individual) and enclosed in tin cups (4×6 mm). From less homogeneous specimens two subsamples were taken. The samples were combusted in an

elemental analyser (NA 1110; Carlo Erba, Milan) interfaced (ConFlo III; Finnigan MAT, Bremen, Germany) to an isotope ratio mass spectrometer (IRMS; Delta Plus; Finnigan MAT). The isotope data are presented as $\delta^{15}N$ (‰) relative to atmospheric nitrogen and $\delta^{13}C$ (‰) relative to Pee Dee Belemnite (PDB) standard and were calculated according to McKinney *et al.* (1950):

$$\delta X = [(R_{sample}/R_{standard}) - 1]$$

where δX is $\delta^{15}N$ or $\delta^{13}C$ and R is the respective $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratio. Each sample was measured against a working standard reference gas which had previously been calibrated against secondary isotope standards (IAEA-N1 and IAEA-N2 for nitrogen; IAEA-CH6 for carbon). Accuracy of calibration was ±0.08‰ SD for nitrogen and ±0.06‰ SD for carbon. Blank determinations were performed routinely before each batch of samples by running empty tin cups. After every tenth sample, a solid internal laboratory standard (SILS; a fine ground bovine horn having a similar C/N ratio than the samples) was run. Precision for SILS measurements during the measurement period was ±0.05‰ SD and ±0.07‰ SD for nitrogen and carbon, respectively. The resulting measurements included the $\delta^{15}N$ and $\delta^{13}C$, the nitrogen and carbon elemental contents, and the carbon-to-nitrogen ratio (C/N). We used subsamples to calculate a mean value for less homogeneous samples. The mass spectrometer results for two of the 16 termite samples proved to be significantly contaminated with soil residues that could not be removed and were therefore eliminated from further analysis.

Results

Nitrogen and carbon isotope signals among termites

Termites collected from 14 mounds were identified to the genus level and comprised mostly *Odontotermes* sp. ($n = 9$), followed by *Trinervitermes* sp. ($n = 4$) and *Macrotermes* sp. ($n = 1$). We found four termite mounds inhabited by *Trinervitermes* individuals that were most likely originally built by *Odontotermes*, but were now in use by *Trinervitermes*. Measurements of $\delta^{13}C$ and $\delta^{15}N$ indicated distinct feeding types among the termites (Fig. 1a). The $\delta^{13}C$ values of all genera clearly showed a C_4-based carbon source ($\delta^{13}C = -11.0$ to -14.3‰), corresponding with the grasses dominating the plains in the Serengeti, on which the termites feed. Individuals of the genus *Odontotermes* had an average $\delta^{15}N$ value of 4.0‰ ± 1.7‰ (SD), of *Trinervitermes* a $\delta^{15}N$ value of 3.9‰ ± 1.5‰ (SD), and of *Macrotermes* a $\delta^{15}N$ value of 2.2‰ ± 0.07‰ (SD).

Nitrogen and carbon isotope signals among spiders

Spiders that were found on the mound or in the chimneys were identified to the family level. Thomisidae (24.0%), Pholcidae (21.0%), and Lycosidae (15.0%) were generally found to be the most abundant, occasionally encountered were Zodariidae, Theridiidae, Araneidae, and Prodidomidae. Of the 33 spiders, eight could not be identified. Again, the $\delta^{13}C$
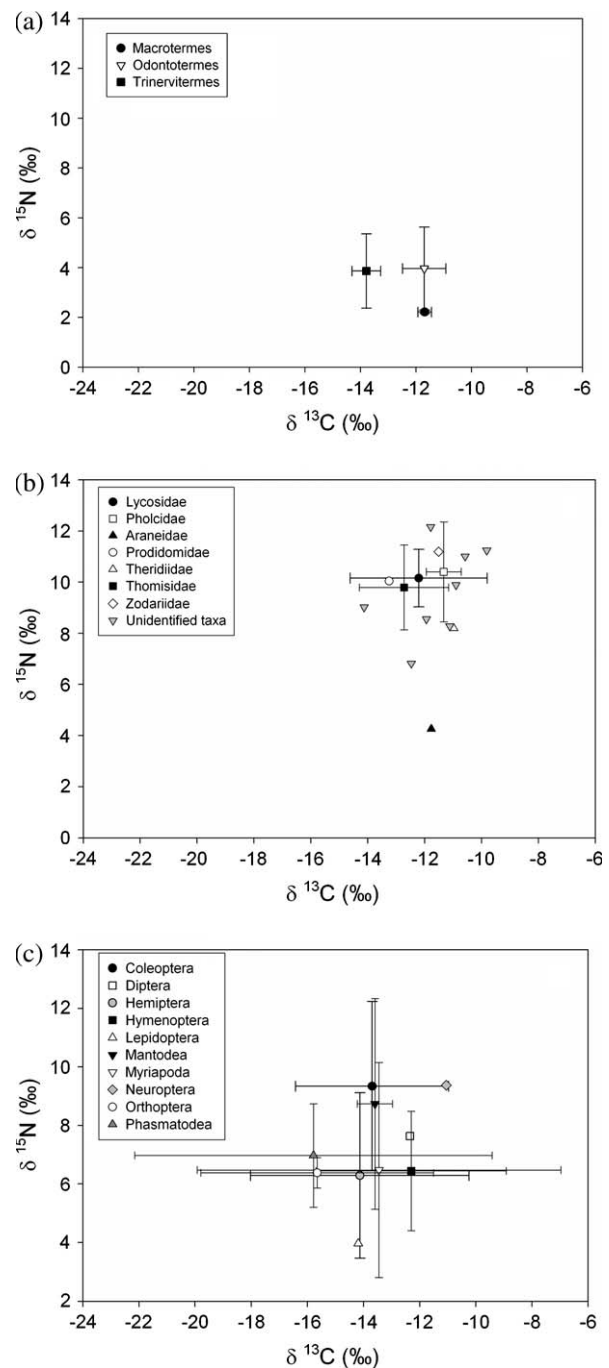

Fig. 1. Means and SDs are plotted for $\delta^{15}N$ and $\delta^{13}C$ (in ‰) of (a) three different termite genera from termitaria ($n = 14$), (b) seven different families of spiders ($n = 34$) found in the termitaria, and (c) 10 different orders of invertebrates other than termites and spiders ($n = 42$) found in the termitaria in the southern grass plains of Serengeti National Park, Tanzania.

values showed a clear C_4-based carbon source ($\delta^{13}C = -9.8$ to -14.6‰) and overall high $\delta^{15}N$ values between 8.0 and 12.4‰ (Fig. 1b).

Nitrogen and carbon isotope signals among other invertebrates

Among the other invertebrates collected from the termitaria were individuals of the orders Coleoptera (26.0%), Hemiptera (23.8%), Hymenoptera (16.6%), Phasmatodea (9.5%), Orthoptera (7.1%), Mantodea (4.8%), and Myriapoda (4.8%). Single individuals were encountered from the orders Diptera, Neuroptera, and Lepidoptera (caterpillar stage). Visual inspection suggested that there was no clear difference in inquiline composition among the mounds of the three termite genera. There was variation in $\delta^{13}C$ and $\delta^{15}N$ among and within individuals of these orders (Fig. 1c). Variation in $\delta^{13}C$ included C_3 as well as C_4 carbon sources. The $\delta^{13}C$ values ranged from −8.8 to a furthest range of −25.2‰ for stick insects (Phasmatodea), indicating a C3 component in the diet of the latter. The $\delta^{15}N$ values ranged from 3.2 to 12.9‰. The herbivorous caterpillars (Lepidoptera), grasshoppers (Orthoptera), some bugs (Hemiptera), and harvester ants (Hymenoptera) showed clearly lower $\delta^{15}N$ values than those of the more carnivorous orders such as the mantids (Mantodea), antlions (Neuroptera), and predaceous beetles of the order Coleoptera. However, most orders contained individuals of different feeding guilds (herbivores, carnivores), resulting in a considerable high within-order variation in $\delta^{15}N$. In addition, the presence of legumes and non-leguminous plants as a food source for herbivorous insects may have caused $\delta^{15}N$ variation within this feeding guild.

Trophic interactions

The $\delta^{15}N$ values of spiders compared with termites of the mound that the spiders inhabited showed that the spiders were on average two trophic levels 6.4‰ ±2.4‰ (SD) higher than the termites, indicating that termites are not a significant com-

ponent of these spiders' diets (Fig. 2). Only three cases out of 34 indicated a possibly direct trophic relation between spiders and termites, based on a $\Delta^{15}N$ of ~3‰: in these cases it concerned a spider of the family Araneidae potentially feeding on individuals of *Odontotermes* sp., one of the family Prodidomidae and one unidentified spider taxon possibly feeding on *Trinervitermes* sp. individuals.

We found eight spider individuals that potentially fed on other invertebrates indicated by their $\delta^{15}N$ signature: these include individuals of the families Thomisidae ($n = 2$), Lycosidae ($n = 2$), Pholcidae ($n = 2$), and two unidentified spider taxa. Their putative prey consisted of individuals of the families Formicidae ($n = 4$), Mantidae ($n = 1$), Acrididae ($n = 2$), Heteronemiidae ($n = 1$), and Myrmeleontidae ($n = 1$) (Table 1). Of these invertebrates, carnivorous individuals of Formicidae ($n = 3$), Mantidae ($n = 1$), and Myrmeleontidae ($n = 1$) appeared to feed on termites (Table 1). Other putative predators of termites were identified as being from the family Reduviidae ($n = 2$), specifically the larvae of these assassin bugs.

Discussion

Our study is the first to reveal, under field conditions, trophic interactions among inquiline invertebrates beyond the occasional observations of single attacks. Stable isotope analysis suggests that spiders are the top predators of the invertebrate food web located in termitaria, but that they rarely feed on termites directly (less than 9% of all individuals). These spiders are in fact two (and sometimes three) trophic levels higher, feeding on other invertebrates that are termitophagous (such as carnivorous ants, mantids, and antlions). Thus, spiders may have a beneficial indirect impact on the termites by feeding directly on termitophagous invertebrates. Hence, within a single given mound we did not merely find a high diversity of trophically
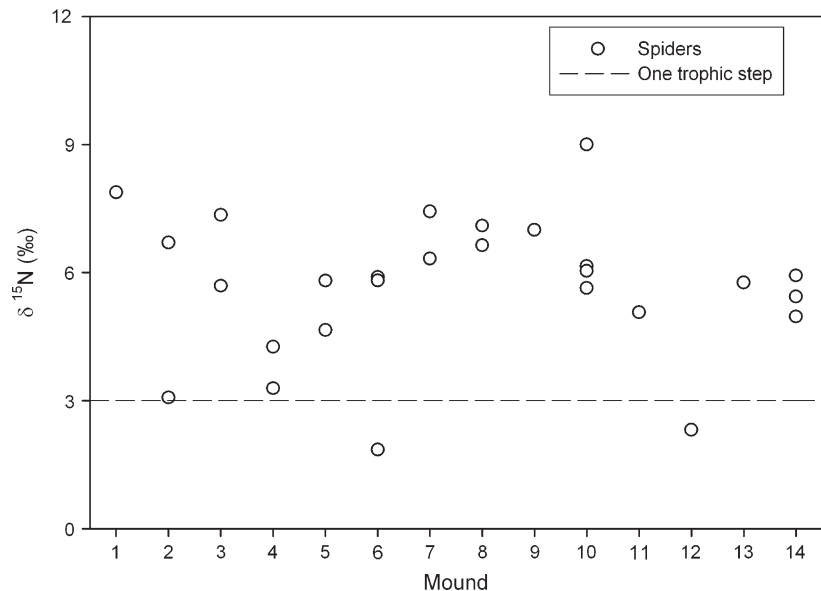

Fig. 2. $\delta^{15}N$ ratios (in ‰) of spiders (of seven families) displayed per mound ($n = 14$) after correcting for $\delta^{15}N$ ratios of the inhabiting termites, in the southern grass plains of Serengeti National Park, Tanzania (open circles). The dashed line indicates a $\delta^{15}N$ signature one trophic level higher than the termites' signature (Δ ~3‰).

Table 1. Description of tentative invertebrate food chains found within termitaria, distinguishing between top predators, secondary consumers and primary consumers. Eleven individuals of spider families had a $\delta^{15}N$ signature one trophic level higher than 10 individuals of other invertebrates (order, family) that themselves were one trophic level higher than termites (genus). All specimens were collected from termitaria ($n = 14$) in the southern grass plains of Serengeti National Park, Tanzania.

Mound	Spiders	Other invertebrates	Termites
1	Thomisidae	Hymenoptera, Formicidae	
2	Unidentified Arachnida	—	*Odontotermes*
3	Lycosidae	Mantodea, Mantidae	Unidentified Isoptera
3		Hemiptera, Reduviidae	Unidentified Isoptera
4	Prodidomidae	—	*Trinervitermes*
5	Lycosidae	Hymenoptera, Formicidae	*Trinervitermes*
5	Thomisidae	Orthoptera, Acrididae	
7	Unidentified Arachnida	Hymenoptera, Formicidae	*Macrotermes*
9	Unidentified Arachnida	Orthoptera, Acrididae	
10	Pholcidae	Hymenoptera, Formicidae	*Odontotermes*
12		Hemiptera, Reduviidae	*Odontotermes*
12	Araneidae	—	*Odontotermes*
14	Pholcidae	Neuroptera, Myrmeleontidae	*Odontotermes*

unconnected invertebrates, but we were able to show in a quantitative way that inquiline invertebrates are part of a food web with the mound-building termites as the essential component.

Overall, we found 13% of all sampled inquiline invertebrate individuals to be putatively predating upon termites, of which one was a termite-specialist, the termite-eating assassin bug (Hemiptera, Reduviidae; McMahan, 1982). Of these 13% spiders contributed a minor role. This is interesting, as spiders are reported to have special termite-catching techniques, which are used for instance in colour marking of spiders (Evans & Gleeson, 1998). Some authors (Oelbermann & Scheu, 2002; Vanderklift & Ponsard, 2003; Rickers *et al.*, 2006; Wise *et al.*, 2006) suggest that spiders display a Δ of 2.16–2.54‰; if we assume this magnitude of Δ, we find no difference in the number of spiders that may have fed directly on termites. We therefore elected to use the more conservative value of Δ 3‰. Our findings support the study conducted by Haddad and Dippenaar-Schoeman (2002) in so far that they found higher spider abundance and diversity in mounds that were left abandoned. This suggests that these spiders do not feed on termites but use the structure of the mound to catch (other) prey. Interestingly, all termite-feeding spiders in our study were ground wandering (actively hunting) spiders. Also, the spiders feeding on other invertebrates were, with an exception for some individuals of the web-building family Pholcidae, ground wandering spiders. Ground dwelling spiders have been mentioned as specialists on the harvester termite *Hodotermes mossambicus* (Dippenaar-Schoeman *et al.*, 1996). The low number of termitophagous spiders in our study may be explained by the fact that the majority of termite species present in our study area are quite inconspicuous and use foraging tunnels to protect them from sunlight, which may lower their risk of becoming prey to spiders. We acknowledge that some of the potential prey of inquiline spiders, such as the more agile flies and mosquitoes, were not sampled in our study. As the sampling was done by daylight, nocturnal invertebrates (e.g. moths) were also not included in the analyses but may contribute to the diet of spiders, especially of the web-building taxa.

In conclusion, our data provide evidence not only for the presence of diverse taxa of invertebrates inside and at the surface of termite mounds, but also for the trophic interactions among these invertebrates. Thus, termitaria may play an important role in enabling localised, open invertebrate food webs. We can, however, draw no explicit conclusions regarding the importance or the differential ecological role of the mounds themselves compared with the surrounding environment given a lack of control data from the surrounding matrix of this area. This study focused on trophic interactions within the physical structure of the termite mounds. We suggest that future studies include trophic interactions of invertebrates in the surrounding environmental matrix for comparisons, allowing broader conclusions with respect to trophic connectiveness of termitaria and the surrounding environment. Trophic interactions in termitaria and surrounding matrix could be explored in different habitat types, where more heterogeneous woodlands may differ significantly in trophic complexity from the open plains. This may provide further support for our hypothesis that termitaria are distinct architectural features creating more heterogeneity in the surrounding landscape, acting in this way as foci of invertebrate trophic interactions.

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