The Potential and Limits of Termites (Isoptera) as Decomposers of Waste Paper Products

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ABSTRACT Termites (Isoptera) have often been proposed as decomposers of lignocellulosic waste, such as paper products, while termite biomass could be harvested for food supplements. Groups of *Coptotermes formosanus* Shiraki and *Reticulitermes speratus* (Kolbe) were kept for 4 and 8 wk, respectively, in the laboratory and given up to 10 different types of paper as their food source. Paper consumption, survival, caste composition, and lipid content were recorded. Corrugated cardboard was by far the most consumed paper product, although survival on it was not necessarily favorable. In *R. speratus*, lipid reserves and neotenic numbers were quite high, but no breeding occurred. Cardboard may be the "junk food" equivalent for termites. Within the tested period, termites did not perform well on paper products that form the bulk of waste paper—-corrugated cardboard, newsprint, and pamphlets and magazines. On all paper products (except recycled office paper), neotenic reproductives were formed, but larvae were observed only on kraft pulp and tissue paper. That all waste paper products contain lignocellulosic fibers does not automatically make them suitable for decomposition by termites. Each paper product has to be assessed on its own merit to see whether termites can reproduce on this diet, if it were to be a candidate for sustainable "termidegradation" and termite biomass production.

KEY WORDS *Coptotermes formosanus*, *Reticulitermes speratus*, paper consumption, termite survival, termite lipid content

In most countries, timber and paper comprise a large proportion of the biodegradable solid waste. For example, in Japan, the world's third largest producer of paper products, the demand for paper and paper board reached 31.6 million tons in 2008 (Japan Paper Association 2010). Large volumes (>19.6 million tons) are recovered as waste paper and become available for different uses. Several options are available to manage such lignocellulosic waste. Although a high percentage of these materials are still deposited in landfills, simply burnt, or used for energy gain, such waste is increasingly recovered and reprocessed into a range of biomaterials (Sathre and Gustafsson 2006). This may include chemical and enzymatic pretreatment and microbial degradation for the production of biofuel, various chemicals, fertilizer, and the like (Kishino et al. 1998, Ohkuma 2003, Fox and Noike 2004, Brune 2007, Sankar Ganesh et al. 2007, Scharf and Boucias 2010).

Alternatively, termites have been proposed as direct agents for bioconversion of lignocellulosic waste (French 1988 in Toninger 1997; Haritos 1992; Haritos et al. 1993, 1994; Myles 1995; Toninger 1997) in contrast to using enzymes from some of their gut microbes (Ohkuma 2003, Brune 2007) because the natural termite diet is cellulose-based. Assumptions about the potential of termites to decompose paper products have been strengthened by the finding that termites are able to metabolize and eliminate toxic lipophilic xenobiotics, as for example, presently found in news print ink (Haritos et al. 1993). However, apart from Toninger (1997), only in more recent times has the actual potential of "termidegradation" (Sankar Ganesh et al. 2007) for solid biodegradable waste moved from theoretical consideration to the experimental stage (Severtson 2006; Sankar Ganesh et al. 2007; Itakura et al. 2008a,b).

Termites are also of notable nutritional value due to their protein and lipid content, including essential amino and fatty acids (Wiegert and Coleman 1970, Carter et al. 1972, Redford and Dorea 1984, Paoletti et al. 2003, Itakura et al. 2006), although higher amounts of some biochemicals, notably lipids, are specific to certain castes such as nymphs and alates (La Fage and Nutting 1978). In fact, termites form an important component in the diet of many animals at certain times of the year, for example, when termite alates are avail-

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able or throughout the seasons. In several regions of the world, humans also supplement their diet with insects, including termites (DeFoliart 1999, Paoletti et al. 2003, Verkerk et al. 2007).

It has been proposed that both aspects of termites, as decomposers and as a source of nutrients, could be combined: maintain and rear termites on cellulose waste products such as paper, harvest the termites, and convert them to food supplements for stock (fish, poultry) or to specific products as dietary supplements for humans (French 1988; Haritos 1992; Toninger 1997; Itakura et al. 2006; Severtson 2006; Sogbesan and Ugwumba 2008a,b).

Termites are indeed capable of attacking a wide range of cellulose-based materials and can inflict damage to other materials without any food value to them, such as plastics, foam board, bitumen, and others, as countless references and reports attest. However, if termites are to be effective decomposers, and the intention is to harvest termite biomass, they not only have to attack the chosen food substrate but also to survive and thrive on it. Subterranean termites are very selective feeders (Lenz 1994). The waste material(s) would have to be of a nutritional quality that allows termites to breed. Only then could termites be harvested in a sustainable way for processing as a food supplement. Various additions to a paper product, such as fillers, coatings, adhesives, toners, dyes, inks, and other chemicals (Lintu 1990; Haritos et al. 1993, 1994; Hess et al. 2001), and decreasing cellulose fiber length (Yoshimura et al. 1993), the more paper pulp is recycled, may pose additional restrictions on the suitability of a waste paper product as a termite diet. The connections of the quality of the waste products with termite survival and reproduction have rarely been considered in proposals to use termites as decomposers and for biomass production (Toninger 1997, Itakura et al. 2006).

Despite earlier recommendations to use termites for the decomposition of waste paper (Haritos 1992, Myles 1995), and indications from a short-term experiment of 2 wk that termites have the ability to detoxify print ink components otherwise deleterious to their health (Haritos et al. 1993, 1994), the willingness of termites to feed on different types of paper has only been investigated a few times (Toninger 1997, Severtson 2006, Sankar Ganesh et al. 2007) and does not seem to be universal. It is still questionable whether paper products, with the exception of various filter papers that are commonly used as a food and water-holding substrates for laboratory experiments with termites (Mauldin and Rich 1975), which do not form a significant part of the paper recycling stream, represent a long-term medium for rearing these insects. Essentially, what impact do these substrates have on termite survival?

We report the results from an investigation into the potential of termites as decomposers of different types of waste paper, by using consumption, survival rate, and lipid content as a measure of physiological condition (La Fage and Nutting 1978, Arquette et al. 2006, Morales-Ramos and Rojas 2007) for laboratory-held groups of *Coptotermes formosanus* Shiraki and *Reticulitermes speratus* (Kolbe). Groups of the latter species also yielded information on the suitability of waste paper products as a rearing substrate.

Table 1. Caste composition (mean ± SE) of 0.5-g samples of *R. speratus* based on counts of 0.2-g samples (presoldiers, soldiers, and neotenics had been removed prior to weighing groups)

Colony	Workers	Nymphs[a]	Larvae[b]	Total[c]
1	278.5 ± 4.4	22.0 ± 3.1	13.0 ± 4.6	313.5 ± 7.7
2	270.5 ± 3.5	11.0 ± 1.3	84.0 ± 7.7	365.5 ± 10.6

[a] The nymph number of colony 1 is significantly different from that of colony 2 ($P < 0.05$; *t*-test).
[b] The larval number of colony 1 is significantly different from that of colony 2 ($P < 0.01$; *t*-test).
[c] Total number in colony 1 is significantly different from that of colony 2 ($P < 0.01$; *t*-test).

Materials and Methods

Termites. *C. formosanus* groups were obtained from two colonies (A and B) held in a climate-controlled room (28 ± 2°C and 80% RH) at the Research Institute for Sustainable Humanosphere (RISH), Kyoto University, Japan (Kubota et al. 2008). They were collected from feeding sites within their holding tanks. Termites, wood, and soil debris were placed on raised platforms within collecting trays. Only termites that walked off on their own from those platforms were used in the study. These foraging parties were comprised of soldiers and mainly mature workers (W5, W5+; see Roisin and Lenz 1999). Groups of mature workers only (0.5 g) were established. Based on the average weight of five randomly selected mature workers from each colony, the 0.5-g groups of colony A were comprised of 156 workers, and those of colony B included 152 workers.

R. speratus was collected from two locations. Colony 1 inhabited pine (*Pinus* spp.) logs lying on the ground in a public park in Uji, Kyoto, Japan. Termites from colony 2 were extracted from a long-term aggregation site on the Uji campus of Kyoto University. To separate termites from soil and wooden debris, layers of damp and crumpled paper towels were placed on top of the materials. Any termites moving into the towels were gently tapped off into holding containers. Presoldiers, soldiers, and neotenics were removed and groups of 0.5 g in the remaining caste composition (workers, nymphs, and larvae of varying stages) were weighed. The number and composition of termites in the 0.5-g samples were determined from counting out 0.2-g samples ($n = 3$). Both colonies differed in the number of nymphs and larvae (Table 1).

Formation of soldiers and neotenics (the latter only in *R. speratus*) in the course of the experiment could be used as further indicators of the suitability of a paper type as a termite diet; hence at the start of the experiments, those castes were excluded from the termite groups.

Paper Types. Ten types of paper were investigated with *R. speratus*, and only a selection of them with *C.*

Table 2. Types of material offered as food sources (denoted by X) to groups from 2 colonies each of *C. formosanus* and *R. speratus*

Type of material	*C. formosanus*		*R. speratus*	
	Colony A	Colony B	Colony 1	Colony 2
High-quality print, 77.9 g/m^2			X	X
High-quality print, 83.7 g/m^2			X	X
Top-quality print, 127.9 g/m^2			X	X
Top-quality print, 127.9 g/m^2, coated	X	X	X	X
Kraft pulp	X	X	X	X
Tissue paper	X		X	X
Recycled office paper	X		X	X
Newsprint	X	X	X	X
Glossy pamphlets	X	X	X	X
Corrugated cardboard	X		X	X
Japanese cedar	X	X	X	X

formosanus because at the time of the experiment, only a limited number of workers was available (Table 2). Several types of quality printing paper, recycled office paper, paper pulp, tissues, newsprint, glossy advertising material, and corrugated cardboard were included (Table 2). Single or multiple layers of sheets of paper products (10 by 7.5 cm; i.e., one eighth of an A4 sheet in area), depending on their weight, were tightly rolled up around a 1.5-mm-diameter metal rod, leaving a central hole once the rod was removed which termites could use to enter the inner part of the paper rolls. The rolls were secured with small pieces of light sticky tape at either end to prevent unfolding. Paper rolls were oven-dried for 24 h at 50°C, weighed and then offered as the sole food (3–4-g lots) to termites. Heavier papers were given in a single roll, lighter papers usually in one larger roll and a smaller one to reach the target weight. Samples of corrugated cardboard were separated into the backing part and the corrugated part; each was weighed individually and offered together as two rolls side by side. Performance on papers was compared with that on Japanese cedar (*Cryptomeria japonica* D. Don.), a timber species routinely used in Japan in laboratory assessments of wood protection systems and various biological studies (e.g., Japanese Industrial Standard JIS K 1571, Japanese Industrial Standard 2004; Ngee et al. 2004; Katsumata et al. 2007). The wood was offered as a row of four blocks, each measuring 2 by 2 by 1 cm, and touching each other with their 2- by 2-cm cross-sectional faces.

Experimental Units. Plastic jars with vented lids (5.8 cm in height; diameter at the base, 9.5 cm; 10.0 cm at the top) were filled with grade 3 vermiculite (15 g) sourced from Australia [Exfoliators (Aust.) Pty. Ltd., Dandenong, Australia]. Distilled water (30 ml) was added to give a 200% moisture content of the matrix. A strip of clear plastic foil (8.0 cm in length, 3.0 cm in width) was placed on the vermiculite surface. The paper rolls or Japanese cedar blocks were positioned on top of the foil. The foil prevented intimate contact of the paper or wood with the moist vermiculite. Termites were added once the materials were in position. Termites could reach the paper or wood by either coming over the edges of the foil from any side, or directly from underneath via three holes that had been punched with an office punch into the foil. For each material, and termite colony, five replicated groups were established.

Groups of *R. speratus* were maintained for 8 wk and due to circumstances those of *C. formosanus* only for 4 wk in a room at 28°C and 80% RH. At the end of the experiment surviving termites of each group were retrieved and their live weight recorded. Termites also were sorted and counted by caste. Paper samples were cleaned, first air-dried for a day, and then oven-dried for 24 h at 50°C. Termites from the five replicates of a given treatment (separated by nymphs and workers in the case of *R. speratus*), were pooled and preserved in 70% ethanol for later lipid analysis.

Lipid Analysis. The preservative (70% aqueous ethanol) used for transporting each sample from Japan to Australia was evaporated under a nitrogen stream, and the termites were dried in a vacuum desiccator at 5 Pa over silica gel. The lipid constituents were quantified by a method similar to that described by Lacey et al. (2010). A small quantity (≈3 mg) of the sample in a screw-capped glass tube (2-ml capacity, polytetrafluoroethylene (PTFE)-faced silicone seal; Alltech, Sydney, Australia) was weighed to the nearest 10 μg by using a 5-figure electronic balance (Ohaus, Melbourne, Australia), and a solution of ethyl *n*-heptadecanoate (500 μg) in absolute ethanol (200 μl) was added as an internal standard. Two glass beads (3 mm in diameter) also were included to facilitate the subsequent solvent extraction.

The headspace was briefly flushed with dry nitrogen and the tightly capped tube was heated at 110°C for 1 h with occasional vortex mixing. The supernatant extract was transferred to a clean screw-capped tube, and ethanol containing 2% sulfuric acid (100 μl) was added. The headspace was briefly flushed with nitrogen, and the tightly capped tube was heated at 110°C for 1 h to trans-esterify the lipids. Any free fatty acids formed by hydrolysis of the lipids also are converted to ethyl esters under these conditions.

Hexane (300 μl) was added at room temperature followed by crushed ice (≈0.5 g) with vortex mixing. The lower aqueous layer was discarded and the hexane solution of the derivatized lipids (mainly glycerides but also some phospholipids) was washed twice with water (300 μl) and dried (with magnesium sulfate).

The solutions of ethyl esters of the fatty acid ligands (principally palmitate, palmitoleate, stearate, oleate, and linoleate) were separated and quantified by gas chromatography (GC) by using a Varian Star 3400 gas chromatograph (Varian, Inc., Palo Alto, CA) with computerized instrument control and data acquisition. The GC capillary column contained a carbowax phase (ECWax: 30 m by 0.32 mm i.d.; phase thickness, 0.25 μm; helium flow, 1 ml/min; on-column injection; 2-m retention gap [Alltech]). The temperature program was 50°C for 1 min; increased at 25°C/min to 170°C, then 5°C/min to 230°C, and remained at 230°C for 2 min. The standard plots for quantification were linear over the range of relative concentrations en-

Table 3. Mean consumption of different paper products and Japanese cedar over 4 wk by 0.5-g groups ($n = 5$) of *C. formosanus*

Type of material	Mean consumption ± SE (g)	
	Colony A	Colony B
Top-quality print, coated	0.279 ± 0.009a	0.279 ± 0.007a
Kraft pulp	0.409 ± 0.005b	0.443 ± 0.016bc
Tissue paper	0.314 ± 0.030ab	
Recycled office paper	0.335 ± 0.013ab	
Newspaper	0.358 ± 0.016ab	0.478 ± 0.011c
Pamphlets	0.355 ± 0.033ab	0.383 ± 0.032b
Corrugated cardboard	1.365 ± 0.014d	
Japanese cedar	0.511 ± 0.031c	0.497 ± 0.022c

Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD test).

Table 4. Mean consumption of the two components of corrugated cardboard, the backing, and the corrugations

Termite species	Mean consumption ± SE (%)	
	Backing	Corrugations
C. formosanus	16.0 ± 1.3	84.0 ± 1.3*
R. speratus	29.5 ± 3.6	70.8 ± 3.6*

Means within the same row with an asterisk (*) denote significant difference ($P < 0.05$; *t*-test).

countered in this study. The quantities of the various ethyl esters were summated to yield an arbitrary measure of the total lipid in the sample.

Data Analysis. Data on consumption, final termite numbers and weights of each paper were subjected to analysis of variance (ANOVA), and means were separated with Tukey's honestly significant difference (HSD) test ($P = 0.05$). Data in percentages were first transformed into arcsine values before ANOVA. Paper consumption rates on the backing and corrugation of corrugated cardboard were compared using Student's *t*-test ($P = 0.05$). All statistical analyses were performed using STATISTIX, version 7.0 (Analytical Software. Tallahassee, FL).

Results and Discussion

The study was conducted with termites from only two colonies of each species. Furthermore, the groups of *C. formosanus* were exposed to the experimental materials for only 4 wk, whereas the response of *R. speratus* was measured for 8 wk. Although these circumstances may restrict a too detailed interpretation of the results, some general patterns are nevertheless very evident on the extent to which the different materials present acceptable food sources for sustained termite maintenance and could be candidates for termidegradation. Measures, such as consumption, survival rates, lipid content, caste development, and indications of breeding, either singly or in combination, are used to characterize the significance of the materials for termites.

C. formosanus. *Paper Consumption.* Groups fed on all paper types offered to them (Table 3). Consumption (0.279 g) by both colonies of coated top quality print was significantly lower ($F_{colony\ A} = 284.55$, df = 7, $P < 0.05$; $F_{colony\ B} = 20.21$, df = 4, $P < 0.05$) than of other papers. Most papers had amounts between 0.314 and 0.478 g removed. Differences between these paper products were either not significant ($P > 0.05$), with the exception of corrugated cardboard (colony A), or as in a couple of cases for colony B. Longer exposure periods beyond 4 wk might have given very different results as indicated from the data for *R. speratus* (see Table 7). Japanese cedar consumption was slightly higher than that for papers, with the exception of corrugated cardboard, ranging from 0.497 to 0.511 g, depending on the colony. The most outstanding result was the consumption of corrugated cardboard: it was eaten by termites from colony A (the only colony to which it was offered) 160% more than Japanese cedar, and at an even higher ratio compared with the other papers (Table 3). *C. formosanus* clearly preferred the corrugations over the backing in a ratio of >5:1 when feeding on the cardboard (Table 4).

Survival. Over a 4-wk experimental period, survival of *C. formosanus* groups was not affected by diet. There were no significant differences in survival either by termite numbers ($F = 3.04$, df = 7, $P > 0.05$) or weight ($F = 2.6$, df = 7, $P > 0.05$) among groups of colony A (Table 5). The high consumption of corrugated cardboard did not improve the condition of the termites. In fact, there were no significant differences in terms of numbers and weight of survivors at the end of the experiment compared with those of other paper types. In colony B, termites survived best on kraft pulp and newspaper after the short experimental period of 4 wk ($F_{weight} = 23.23$, df = 4, $P < 0.05$; $F_{number} = 11.26$, df = 4, $P < 0.05$). Over the 4-wk period, termites also managed to keep the papers largely free of microbial growth.

Caste Composition. Groups of termites on all materials had produced a small number of presoldiers and soldiers after 4 wk (Table 6). The experimental time of 4 wk was too short for groups to reach their final soldier proportion, which for this species is ≈10% (Haverty 1977), and to ascertain any potential effect of diet on the caste composition.

R. speratus. *Paper Consumption.* Groups from both colonies of *R. speratus* fed on all papers types and responded in a similar way except for newsprint and Japanese cedar. (Table 7). High-quality print papers with lower fiber content and recycled office paper and Japanese cedar (the latter only for colony 1) were the least consumed, with mean values ranging from 0.616 to 0.696 g ($F_{colony\ 1} = 14.09$, df = 10, $P < 0.05$; $F_{colony\ 2} = 21.56$, df = 10, $P < 0.05$). Termites ate between 0.761 and 1.003 g from top quality print with a high fiber content, kraft pulp, tissue paper, newsprint, pamphlets and Japanese cedar (colony 2). In contrast to *C. formosanus, R. speratus* fed well on top-quality print. Corrugated cardboard was, as in *C. formosanus*, the preferred food item with significantly higher amounts removed (1.317–1.475 g) than of any other material.

Survival. In general, survival of *R. speratus* in laboratory groups is lower than that of *C. formosanus*

Table 5. Mean survival ± SE by termite wt and numbers of 0.5-g groups ($n = 5$) of *C. formosanus* after 4 wk of feeding on different paper products

Type of material	Colony A		Colony B	
	Mean wt ± SE (%)	Mean no. ± SE (%)	Mean wt ± SE (%)	Mean no. ± SE (%)
Top-quality print, coated	67.2 ± 3.3a	82.9 ± 3.4a	57.2 ± 2.2a	75.3 ± 3.1a
Kraft pulp	77.4 ± 2.8a	93.7 ± 2.2a	78.6 ± 0.9c	92.0 ± 0.7b
Tissue paper	81.0 ± 2.7a	95.9 ± 1.6a		
Recycled office paper	51.1 ± 10.9a	63.6 ± 13.8a		
Newspaper	75.0 ± 2.7a	94.1 ± 2.4a	70.9 ± 1.2bc	88.0 ± 1.0a
Pamphlets	53.4 ± 5.4a	69.5 ± 8.1a	59.2 ± 0.7a	77.6 ± 1.1b
Corrugated cardboard	79.0 ± 1.6a	95.3 ± 1.6a		
Japanese cedar	61.8 ± 13.4a	72.4 ± 16.0a	63.7 ± 3.0ab	76.0 ± 3.8b

Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD test).

(e.g., Kubota et al. 2007). Survival of *R. speratus* groups after 8 wk on a diet of paper products was notably diverse, whether they were compared by weight ($F_{\text{colony 1}} = 47.18$, df = 10, $P < 0.05$; $F_{\text{colony 2}} = 73.04$, df = 10, $P < 0.05$) or by numbers ($F_{\text{colony 1}} = 56.88$, df = 10, $P < 0.05$; $F_{\text{colony 2}} = 68.69$, df = 10, $P < 0.05$). Most groups on recycled office paper were dead after 8 wk. The quality print papers, pamphlets, and Japanese cedar resulted in survival rates (by weight or numbers of termites) below 10% in the case of colony 1, with no significant differences ($P > 0.05$) in survival among those six materials (Table 8). In colony 2, survival on these materials was similarly low except for uncoated top-quality print and pamphlets. On these papers, between 10 and 20% of termites survived.

Termites kept on newspaper (both colonies) and corrugated cardboard (colony 2) fared better with significantly ($P < 0.05$) higher but still overall low survival rates (weight) of between 22.5 and 38.6% than on the other above-mentioned materials. On corrugated cardboard, survival for groups of colony 2 was in the similar high range of the two products, kraft pulp, and tissue paper, on which groups from both colonies survived best, with values between 62.2 and 75.2%. These high survival rates were significantly different from those on any other material (Table 8).

In this experiment, *R. speratus* groups were kept at 28°C, above the more commonly used 25°C for longer-term maintenance of groups of this species (e.g., Matsuura and Nishida 2001). Termite maintenance at somewhat elevated temperatures tends to lower survival but increase food consumption rates (Lenz et al. 1987, Smith and Rust 1993).

On paper samples with poor termite survival rates, often microfungi (*Trichoderma*, *Aspergillus*, and others) and bacterial *Serratia* could establish themselves over time. Termites were no longer able to keep the paper surfaces clean from microbes. Once the fungi started to sporulate they may have become toxic or repellent (Lenz 1969, Heintschel et al. 2007). In replicates with significantly contaminated paper, termites either retreated to the central tunnel in the roll and often sealed themselves into this smaller space or more or less avoided the papers and stayed in the vermiculite. In such cases, survival rates will have been affected by a combination of an inadequate diet and exposure to sublethal or even lethal compounds of microbial origin. Interestingly, if such groups included neotenics, they were disproportionately represented among the survivors (Table 9).

Lipid Content. Only the results for *R. speratus* are provided (Table 9). The short experimental period of 4 wk in *C. formosanus*, and the limited number of paper type and colony combinations under trial did not allow too many conclusions to be drawn.

In general, nymphs contained greater stores of lipids than workers (21–38% of dry weight and 12–17%, respectively) at the start of the experiment, in line with what is generally reported for these two castes (Redford and Dorea 1984, La Fage and Nutting 1978, Waller and La Fage 1987, Itakura et al.

Table 6. Mean caste composition numbers ± SE of 0.5-g groups ($n = 5$) of *C. formosanus* workers after feeding for 4 wk on different paper products

Type of material	Colony A[a]		Colony B[b]	
	Workers	Soldiers	Workers	Soldiers
Top-quality print, coated	125.6 ± 5.5a	3.8 ± 0.5ab	112.0 ± 4.5a	2.5 ± 0.3ab
Kraft pulp	142.0 ± 3.2a	4.2 ± 0.4ab	136.8 ± 1.0b	2.7 ± 0.6ab
Tissue paper	145.6 ± 2.1a	4.0 ± 0.5ab		
Recycled office paper	95.4 ± 20.5a	3.8 ± 1.3ab		
Newspaper	142.2 ± 4.2a	4.6 ± 0.7a	130.8 ± 1.6b	2.8 ± 0.5a
Pamphlets	105.6 ± 12.4a	2.8 ± 0.6ab	116.2 ± 1.7a	1.8 ± 0.2ab
Corrugated cardboard	143.0 ± 3.0a	5.6 ± 0.8a		
Japanese cedar	112.0 ± 24.7a	1.0 ± 0.8b	114.8 ± 5.6a	1.0 ± 0.4b

Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD test).
[a] Initial worker number, 156; initial soldier number, 0.
[b] Initial worker number, 152; initial soldier number, 0.

Table 7. Mean consumption (in grams) of different paper products and Japanese cedar over 8 wk by 0.5-g groups ($n = 5$) of *R. speratus*

Type of material	Mean consumption ± SE	
	Colony 1	Colony 2
High-quality 77.9	0.662 ± 0.012ab	0.556 ± 0.021a
High-quality 83.7	0.687 ± 0.030abc	0.696 ± 0.066abc
Top-quality print	1.003 ± 0.031d	0.986 ± 0.028d
Same-but-coated	0.836 ± 0.089abcd	0.828 ± 0.098bcd
Kraft pulp	0.868 ± 0.024bcd	0.761 ± 0.021abc
Tissue paper	0.866 ± 0.056bcd	0.812 ± 0.035bcd
Recycled office paper	0.616 ± 0.007a	0.617 ± 0.031ab
Newspaper	0.947 ± 0.056d	0.753 ± 0.026abc
Pamphlets	0.908 ± 0.048cd	0.881 ± 0.074cd
Corrugated cardboard	1.475 ± 0.027e	1.317 ± 0.018e
Japanese cedar	0.696 ± 0.066abc	0.938 ± 0.040cd

Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD test).

2006), although specifically our values for *R. speratus* are lower than those mentioned by Itakura et al. (2006). Oleate was the fatty acid ligand present in the highest proportion.

On paper products that enabled termites to survive at high rates of >60% (Table 8), such as kraft pulp, tissue paper, and corrugated cardboard (colony 2), lipid content of workers and nymphs was at or even exceeded the initial levels in the termites (Table 9). An increase in total lipids also has been reported for field collected *R. flavipes* after being maintained for several weeks in the laboratory (Arquette et al. 2006). On newspaper with survival rates of 23–39%, lipid content dropped to 5.8–6.8% by weight in workers, but nymphs retained their high percentages of 38–44%. A diet of corrugated cardboard gave survival rates between 26 and 68% (colony 1 and colony 2, respectively), and lipid stores remained high or even increased over those present in termites at the beginning (≈20% for workers and 37–41% in nymphs).

Very low termite survival was seen on the quality print papers, pamphlets, and Japanese cedar paralleled by low values for lipids of <10% in workers and <20% in nymphs (with the exception of nymphs from colony 1 on pamphlets with 26% lipids).

Although it seems that overall high or low survival rates on a diet of paper products are matched by the amount of lipid stores in workers and far less pronounced in nymphs, the pattern is not universal as the example of termites kept on newspaper illustrates: survival rates were relatively high, yet lipids in workers were as low as in workers on far more unfavorable diets. This may well indicate that the capacity of termites to detoxify print ink components (Haritos 1992; Haritos et al. 1993, 1994) functions adequately over shorter periods of a couple of weeks, but prolonged exposure to such a diet significantly affects metabolic activity and leads to a depletion of energy reserves.

Caste Composition. At the start of the experiment, all presoldiers, soldiers and neotenics were removed from groups. This allowed assessment whether or not the type of diet might influence success in forming new soldiers and replacement reproductives (Table 10).

Soldiers. The natural soldier proportion in mature colonies of *R. speratus* is 2.5% (Matsuura 2002). With the relatively small initial group size of on average 340 termites only a few soldiers could be expected in the group after 8 wk. The entire process of reaching a balanced ratio between soldiers and the other castes might exceed the experimental period. In the experimental groups, only a small number of soldiers, in total 18, had been produced, and many groups across all paper products were without any soldiers (Table 10). Soldier numbers between paper types were not significantly ($P > 0.05$) different. However, survivors in groups kept on a diet of higher quality print and Japanese cedar failed to have any soldiers, clearly a reflection of low survival rates overall. Groups on kraft pulp and tissue paper with high termite survival were more likely to include a soldier (and in one replicate of kraft pulp even two) after 8 wk. With newspaper and pamphlets as the food source, despite relatively low survival of termites, some groups contained a soldier after 8 wk. Groups from colony 2 on corrugated cardboard lacked a soldier despite high termite survival, whereas a few replicates contained a soldier in colony 1 despite much lower survival rates.

Table 8. Mean percentage survival (± SE) by termite weight and numbers of 0.5-g groups ($n = 5$) of *R. speratus* after 8 wk of feeding on different paper products

Type of material	Colony 1		Colony 2	
	Mean wt ± SE (%)	Mean numbers ± SE (%)	Mean wt ± SE (%)	Mean numbers ± SE (%)
High-quality 77.9	3.6 ± 1.5a	2.9 ± 1.1a	4.2 ± 1.5ab	3.5 ± 1.4abc
High-quality 83.7	3.6 ± 1.5a	3.1 ± 1.1a	3.3 ± 1.0ab	2.8 ± 0.9ab
Top-quality print	2.0 ± 1.2a	1.7 ± 1.1a	16.0 ± 3.8ab	12.2 ± 2.8abc
Same, coated	0.7 ± 0.7a	0.7 ± 0.7a	1.8 ± 1.6ab	1.5 ± 1.4a
Kraft pulp	75.2 ± 2.5d	66.5 ± 3.0d	74.4 ± 1.2d	59.2 ± 1.1e
Tissue paper	64.4 ± 6.0d	54.8 ± 3.8d	62.2 ± 7.0d	46.1 ± 4.4d
Recycled office paper	0a	0a	0.2 ± 0.2a	0.2 ± 0.2a
Newspaper	38.6 ± 9.1c	31.7 ± 7.4c	22.5 ± 3.6c	16.0 ± 2.5c
Pamphlets	10.7 ± 4.8ab	8.8 ± 3.8ab	17.4 ± 1.7bc	15.1 ± 1.8bc
Corrugated cardboard	25.9 ± 4.5bc	20.2 ± 3.5bc	67.7 ± 6.0d	49.2 ± 5.8de
Japanese cedar	0.5 ± 0.5a	0.3 ± 0.3a	5.5 ± 0.8ab	2.4 ± 0.3a

Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD test).

Table 9. Lipid content (in percentage body dry weight) of workers and nymphs of *R. speratus* kept for 8 wk on different paper products and Japanese cedar

Colony	Workers						Nymphs					
	Palmitate	Palmitoleate	Stearate	Oleate	Linoleate	Total lipids	Palmitate	Palmitoleate	Stearate	Oleate	Linoleate	Total lipids
At start of exp												
1	1.26	0.12	1.44	7.54	1.73	12.09	6.35	0.11	2.64	24.73	4.70	38.53
2	1.70	0.20	1.99	11.38	1.79	17.06	3.42	0.11	1.55	13.98	2.64	21.70
High-quality print 77.9 g												
1	1.42	0.07	0.78	5.91	1.02	9.20			N.A.[a]			
2	0.86	0.11	0.62	4.05	0.59	6.23	2.63	0.15	1.48	10.58	1.68	16.52
High-quality print 83.7 g												
1	0.10	0.01	0.12	0.28	0.14	0.65			N.A.			
2	0.79	0.10	0.61	3.50	0.73	5.73	2.63	0.15	1.48	10.58	1.68	16.52
Top-quality print 127.9 g												
1	0.36	0.02	0.26	1.27	0.41	2.32			N.A.			
2	0.56	0.13	0.46	3.47	0.58	5.20			N.A.			
Top-quality print 127.9 g, coated												
1			N.A.						N.A.			
2	0.29	0.05	0.23	1.10	0.27	1.94			N.A.			
Kraft pulp												
1	2.31	0.16	1.52	10.73	1.78	16.50	9.00	0.10	6.20	20.50	1.80	37.60
2	3.41	0.37	1.96	18.03	2.49	26.26	6.96	0.42	3.53	28.23	4.36	43.50
Tissue paper												
1	2.25	0.22	1.59	12.44	1.50	18.00	8.60	0.20	6.90	25.60	0.70	42.00
2	2.40	0.27	1.58	12.12	1.63	18.00	4.79	0.22	2.98	19.37	3.44	30.80
Newspaper												
1	0.72	0.10	0.63	4.41	0.90	6.76	5.00	1.10	5.20	22.70	4.70	38.70
2	0.59	0.11	0.53	3.86	0.74	5.83	6.42	0.34	3.46	28.61	5.22	44.05
Pamphlets												
1	1.17	0.12	0.77	5.76	1.21	9.03	3.10	0.90	3.00	14.4	4.70	26.10
2	1.04	0.19	0.76	6.27	0.91	9.17	1.16	0.11	0.77	5.57	1.13	8.74
Corrugated cardboard												
1	2.08	0.23	1.79	13.40	1.81	19.31	4.50	0.70	4.70	22.80	4.20	36.90
2	2.57	0.33	1.88	15.07	1.84	21.69	6.29	0.47	6.61	24.53	2.94	40.84
Japanese cedar												
1			N.A.						N.A.			
2	0.81	0.04	0.40	0.28	0.09	1.62			N.A.			

Samples were pooled from all replicates/paper type with survivors. Note that groups kept on recycled office paper were either dead after 8 wk or had an insufficient number of survivors for lipid analysis (see Tables 8 and 10).

[a] N.A., not analyzed because sample size too small (see Table 10).

Interestingly, only eight soldiers were derived from workers, whereas 10 soldiers had developed from nymphs. In experiments with juvenile hormone analogs, nymphs of *Heterotermes indicola* (Wasmann), another rhinotermitid, responded faster and probably to lower doses than workers in developing into well-formed soldiers (Lenz 1976). Some paper products have been known to include a so-called "paper factor," i.e., juvenile hormone analogs of plant origin, which can affect insect development (Sláma and Williams 1965). On kraft pulp, one nymph soldier each was present in four groups, on tissue paper in three groups, on pamphlets in two groups and on top-quality print in one replicate. In only one case (on kraft pulp) was a normal soldier present as well. It is very likely that some of the paper products exerted some low-level influence on soldier production, in this case causing the production of nymph soldiers.

Neotenics and Reproduction. Species of *Reticulitermes* in groups isolated from their colony readily form neotenics and commence breeding, i.e., reestablishing as a colony (Thorne 1998, Lainé and Wright 2003, Miyata et al. 2004, Lenz 2006). Neotenics can develop from workers or nymphs, although nymph-derived neotenics are more common in *R. speratus* (Miyata et al. 2004).

On all paper products with surviving termites, neotenics were present after 8 wk in some replicate groups (Table 10). The highest numbers were recorded on paper pulp, tissue paper, and corrugated cardboard, and, depending on colony, newspaper and pamphlets. Overall, 93.7% of neotenics (out of a total of 144 alive after 8 wk) were derived from nymphs. Females exceeded males in a ratio of 4.5:1. Not surprisingly, groups of colony 1 with double the average number of nymphs as the dominant precursor stage at the start of the experiment (Tables 1 and 10) produced more neotenics than those of colony 2.

Groups of colony 1 commenced breeding, judging by the presence of eggs and larvae on tissue paper, kraft pulp, and to a lesser extent on newspaper and pamphlets. Groups of colony 2 laid only a few eggs on coated top-quality print, pamphlets, and corrugated cardboard (Table 10). The more comprehensive onset of breeding in colony 1 could, in part, be explained by more intense development of neotenics due to higher nymph numbers and a much lower load of larvae to be cared for at the start of the experiment compared with colony 2. Groups from the latter colony included 4 times the number of larvae (Tables 1 and 10) at the start of the experiment compared with colony 1.

Termites as Decomposers of Paper Products. The results indicate that several types of paper could be suitable for breeding. However, negative impacts on termites of several of the paper diets; notably those that compose the bulk of paper waste such as cardboard, newsprint, and magazines (Noda 2002), were observed. Overall, survival of groups may have been

Table 10. Mean final caste composition of groups of *R. speratus* ($n = 5$) after feeding for 8 wk on different paper products and Japanese cedar

Type of material	Mean no. ± SE						
	Workers	Soldiers	Nymphs	♂ Neotenics	♀ Neotenics	Larvae	Eggs
Colony 1[a]							
High-quality 77.9	6.2 ± 2.5a	0a	1.2 ± 0.8a	0.4 ± 0.2a	1.6 ± 0.6ab	0a	0a
High-quality 83.7	7.2 ± 3.1a	0a	1.2 ± 0.6a	0.4 ± 0.2a	0.8 ± 0.4ab	0a	0a
Top-quality print	3.4 ± 2.9a	0a	1.2 ± 1.0a	0.2 ± 0.2a	0.6 ± 0.6a	0a	0a
Same, coated	1.2 ± 1.2a	0a	0.5 ± 0.5a	0.2 ± 0.2a	0.4 ± 0.4a	0a	0a
Kraft pulp	191.2 ± 12.2d	0.6 ± 0.4a	12.0 ± 2.9c	1.0 ± 0.3a	3.4 ± 0.5b	0.6 ± 0.4ab	15.0 ± 8.9a
Tissue paper	153.0 ± 11.4d	0.4 ± 0.2a	13.0 ± 1.0c	0.6 ± 0.4a	2.2 ± 0.8ab	3.0 ± 1.8b	35.0 ± 20.7b
Recycled paper	0a	0a	0a	0a	0a	0a	0a
Newspaper	87.6 ± 21.9c	0.6 ± 0.4a	9.0 ± 2.2bc	1.0 ± 0a	1.4 ± 0.5ab	0.2 ± 0.2a	2.0 ± 2.0a
Pamphlets	22.6 ± 10.1ab	0.6 ± 0.4a	3.0 ± 1.2ab	0.2 ± 0.2a	1.4 ± 0.7ab	0a	0.2 ± 0.2a
Corrugated cardboard	56.8 ± 8.8.bc	0.2 ± 0.2a	4.6 ± 2.2ab	1.2 ± 0.5a	2.6 ± 0.7ab	0a	0a
Japanese cedar	0a	0a	0a	0a	0.2 ± 0.2a	0a	0a
Colony 2[b]							
High-quality 77.9	7.0 ± 4.2ab	0a	3.0 ± 1.2a	0.2 ± 0.2a	0.6 ± 0.2abc	0	0a
High-quality 83.7	7.6 ± 2.2ab	0a	1.4 ± 0.5a	0a	0.4 ± 0.2ab	0	0a
Top-quality print	36.0 ± 7.6ab	0.2 ± 0.2a	7.4 ± 2.7a	0a	1.2 ± 0.2abc	0	0a
Same, coated	3.8 ± 3.8a	0a	1.4 ± 1.2a	0a	0.4 ± 0.2ab	0	0.4 ± 0.4a
Kraft pulp	179.8 ± 6.7c	0.4 ± 0.2a	36.2 ± 3.7c	0.2 ± 0.2a	0.2 ± 0.2ab	0	0a
Tissue paper	139.2 ± 18.0c	0.4 ± 0.2a	31.6 ± 3.0bc	0.4 ± 0.2a	2.2 ± 0.7c	0	0a
Recycled paper	0.4 ± 0.4a	0a	0.2 ± 0.2a	0a	0a	0	0a
Newspaper	35.2 ± 7.6ab	0.4 ± 0.2a	21.0 ± 2.4b	0.2 ± 0.2a	1.8 ± 0.4bc	0	0a
Pamphlets	46.8 ± 6.2b	0.2 ± 0.2a	6.8 ± 1.0a	0.2 ± 0.2a	1.4 ± 0.5abc	0	0.2 ± 0.2a
Corrugated cardboard	149.6 ± 16.6c	0a	29.0 ± 5.5bc	0.2 ± 0.2a	1.4 ± 0.4abc	0	0.2 ± 0.2a
Japanese cedar	1.6 ± 1.4a	0a	6.2 ± 1.0a	0.2 ± 0.2a	0.6 ± 0.2abc	0	0a

Means of the same colony followed by different letters within the same column are significantly different (Tukey's HSD test; $P < 0.05$).
[a] Mean initial caste composition. Colony 1: workers, 278.5 ± 4.4; nymphs; 22.0 ± 3.1; larvae; 13.0 ± 4.6; and total, 313.5 ± 7.7.
[b] Mean initial caste composition. Colony 2: workers, 270.5 ± 3.5; nymphs, 11.0 ± 1.3; larvae, 84.0 ± 7.7; and total, 365.5 ± 10.6.

limited due to paper types either being nutritionally inadequate or containing compounds with sublethal or lethal effects even if otherwise adequate. This poses restrictions on the types of paper materials on which termites could be maintained, bred, and then harvested in a sustainable way.

Corrugated cardboard provides an interesting example of the possible complexities involved. On the one hand, it is consumed at the highest rate of any of the tested paper types by both *C. formosanus* and *R. speratus,* and in the latter species it enabled both workers and especially nymphs to attain or retain high lipid reserves (Table 9), an important factor in assisting breeding (Morales-Ramos and Rojas 2007); yet, termite survival was not necessarily high on this diet (Tables 5 and 8). Within the time frame of 8 wk, there was development of a good number of neotenics, yet almost no actual breeding. In addition, differences in the response of individual colonies of a given termite species were observed. Corrugated cardboard is readily fed upon and is commonly used in the field with great success as an attractive food matrix in devices for monitoring termite presence and activity, yet if it has limited benefit to the consuming termites, it may be the "junk food" equivalent for them.

Discussions about the potential of termites to decompose "waste paper" are based on the assumption that the different products covered under this generic term have cellulose fiber as the common denominator; hence, they should form a very suitable termite diet. However, this alone does not automatically render them as a termite food on which decomposition of such waste and termite biomass production can be based. Natural lignocellulosic "waste" such as dead and fallen wood has a suite of decomposer organisms, notably fungi, wood-boring beetles, termites, and others, acting on their own, in conjunction or succession. Fungi often break down secondary compounds that may be deleterious to termites (Rayner and Boddy 1988, Breznak and Brune 1994, Lenz 1994), thus enabling termites to use the wood resource without or only limited impediment. However, in the production processes of the diverse types of paper, various compounds are added depending on the end use specifications for a given paper product, some with no or little impact on termite health, whereas others will impair termite activity. Termites may only have limited abilities to deal with some of these compounds, even if they can detoxify some (Haritos et al. 1993, 1994), at least over short periods. Paper products resembling more closely natural wood waste, that is, those with the least chemical modification and additions to the wood pulp, are the more likely candidates in the waste paper stream for decomposition by termites.

Myles (2000) discussed the decomposer potential of North American termites. However, the initial emphasis would have to be on identifying specific waste materials of adequate quality and suitability as long-term food sources for termites rather than discussing paper waste products as a generic unit for decomposition. Consumption rates of paper products from relatively short-term laboratory studies used as a basis for estimating lignocellulosic waste product bioconversion of scaled-up laboratory cultures of termites (Tonginger 1997, Severtson 2006) are very likely to give a far too optimistic picture. For example, a colony of the Australian *Coptotermes acinaciformis* (Froggatt) consumed newsprint, glossy magazines, and office paper quite readily in the presence of a diet of favored wood in the laboratory, but comparatively much smaller amounts were eaten when those papers were offered in the field (Severtson 2006). The impact of nonlignocellulosic compounds in paper products can be deleterious on termites, and in turn their bioaccumulation may impact consumers of termite-derived products (Toninger 1997, Severtson 2006). Based on published data and our own results, only certain lines in the waste paper stream may be suitable for larger scale decomposition by termites.

At any given time, a field colony of subterranean termites feeds on a multitude of food sources (Ratcliffe and Greaves 1940) adjusting the variety and proportions of items consumed, such as sound wood and wood modified to varying degrees by microbes, according to colony needs (Lenz 1994). The better the quality of the diet, the more termites are able to compensate for the impact of adverse food constituents (Lenz 1976). This would indicate that if paper products were to be the staple diet for termite mass cultures, food supplements may have to be provided as well. For example, the success of laboratory cultures of wood-feeding termites can be greatly improved if their basic diet of sound wood is supplemented with wood moderately decayed by certain fungi (Becker 1969).

Among various types of solid waste, such as leaves from different tree species, coconut shells, sawdust, waste paper, and cardboard, field colonies of four species of fungus-culturing termites (*Macrotermes, Odontotermes,* and *Hypotermes*) in India fed on waste paper only in relatively small amounts, whereas cardboard and tissue paper were more preferred (Sankar Ganesh et al. 2007). The combined enzymatic activities of termites and the fungus cultures may provide a better path for the breakdown and conversion of cellulose-based waste materials. Alternatively, the use of enzyme systems from termite symbionts and termites themselves (Ohkuma 2003, Brune 2007, Scharf and Boucias 2010, Todaka et al. 2010) may be a far more realistic and promising avenue for dealing with large volumes of lignocellulosic waste products.

In the search for a suitable cellulose-based culture medium for termites with termite biomass production in mind, Itakura et al. (2008a,b) investigated the waste of cultures of the edible mushroom *Hypsizigus marmoreus* (Peck) grown on a mixture of sawdust from *C. japonica* and *Pinus densiflora* Sieb. et Zucc. The investigation gave encouraging early results with increased neotenic numbers over controls and commencement of egg laying within 8 wk. However, in more extended trials the medium also proved unsuitable, and termite vigor declined with time (S. Itakura, personal communication).

In conclusion, "waste paper" comprises diverse products. In this study, termites fed on the full range of materials, in the longer term only a few of such products, such as craft pulp and tissue paper, proved suitable as a staple diet of termite cultures, and for termite breeding. Although paper consumption rates from several weeks of laboratory trials may encourage the idea that termites could be potential major decomposers of a wide range of waste products, survival rates, physiological condition (e.g., lipid content) and the ability of termites to reproduce on such a diet are the critical aspects on which the suitability of a paper type for decomposition, and for termite breeding, has to be based.

The bulk of waste paper is made up of cardboard, newsprint and magazines. In our experiments with *R. speratus,* termites did not fare very well on these three products despite consuming cardboard in much larger amounts than any other type of paper. Termites did not fare any better on a variety of other paper types. Most paper products are clearly not a medium for rearing termites and cannot be used as a basis for the production of termite biomass unless various chemicals deleterious to termites, that are added during the manufacture of different papers, are first removed. Hence, many issues, especially the processes required and the economics involved, may limit using termites directly for paper decomposition and waste paper as a medium for the mass production of termites as a food supplement.

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