

Habitat-specific life-history variation in the Caribbean termite *Nasutitermes acajutlae* (Isoptera: Termitidae)

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Abstract. 1. Population and individual colony characteristics of *Nasutitermes acajutlae* on St John, U.S. Virgin Islands were studied over a 5-year period.

2. Four habitat types (dry forests, moist forests, sparse vegetation, and woodlands) were sampled for *N. acajutlae*, using quadrat-based methods. Lying dead wood was also quantified in the same sites.

3. Habitats differed significantly in the volume of lying dead wood, and total termite nest volume within quadrats was positively related to wood volume. It was hypothesised that the volume of dead wood affected growth, reproduction, and yearly survival of individual colonies.

4. In a sample of > 100 colonies assessed in 1998, 2000, 2001, and 2002, no significant differences in the growth rate of colonies (= increase in nest volume) could be found between habitat types; however, colonies in sparse vegetation were smaller, less likely to survive, and reproduced at a smaller size compared with those in the other three habitats.

5. Overall nest volume in sparse vegetation was high, compared with dry and moist forest, but colonies showed, on average, poorer survival (interpreted as lower fitness), and produced alates at an early stage of development. Optimum habitat characteristics for *N. acajutlae* may include not only favourable microclimate but also the reliable acquisition of new dead wood after storms.

Key words. Dead wood, habitat, individual fitness, life history, *Nasutitermes acajutlae*, population, survival.

Introduction

Termites are one of the most important degraders in tropical ecosystems (Wood & Sands, 1978), and are thought to be responsible for as much as 20% of carbon mineralisation (Bignell & Eggleton, 2000). They are widely distributed on the globe, with highest diversity and densities reported from the neotropics and the African tropics (Eggleton, 2000). Decomposers play an important role in nutrient cycling and energy flux in an ecosystem, and thereby are known to structure communities (Facelli & Pickett, 1991; Scholwaller, 1994; McSorley, 1997; Mikola *et al.*, 2001). Therefore, factors affecting decomposer population dynamics and

individual behaviour may impact processes at higher orders of organisation, and may also vary among habitats with differing resource availability. Studies of different termite species indicate that termite distribution may be regulated by a variety of biotic and abiotic factors acting at different spatial scales (reviewed in Eggleton, 2000). Numerous studies document the density and distribution patterns of termite colonies (e.g. Crist, 1998; Korb & Linsenmair, 1998, 2001), composition of termite communities, their role in ecosystems (reviewed in Bignell & Eggleton, 2000), and the factors that affect their population dynamics (Lepage & Darlington, 2000). Factors found to influence termite populations include predation (Korb & Linsenmair, 2002), competition (Korb & Linsenmair, 2001), temperature (Korb & Linsenmair, 1998), food resources, moisture, and habitat characteristics (reviewed by Lepage & Darlington, 2000).

Despite numerous studies on termite population dynamics, only a few investigate life-history characteristics and fitness

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consequences of individual colonies (e.g. Abe, 1987; Nalepa, 1990). Moreover, studies analysing life-history responses of colonies in different habitats varying in key biotic or abiotic parameters are also uncommon (e.g. Korb & Linsenmair, 1999). The majority of the studies reviewed by Lepage and Darlington (2000) are on subterranean termite species; similar studies on arboreal nesting *Nasutitermes* sp. are uncommon (e.g. Leponce *et al.*, 1995).

Key population (termite nest volume) and life-history parameters (growth, survival, and reproduction) of the arboreal nesting termite *Nasutitermes acajutlae* (Holmgren) were studied in different habitat types. *Nasutitermes* (Termitidae: Nasutitermitinae) is the largest of all isopteran genera, represented by 74 described species from the neotropics alone (Constantino, 1992). As in many eusocial organisms, *N. acajutlae* has distinct morphological castes. In this genus, the castes consist of workers, soldiers, and reproductives (Thorne, 1985; Roisin & Pasteels, 1986). Most members of the worker caste are sterile females that build and maintain the nest, forage, feed the larvae and other castes, and aid in reproduction. Soldiers in this genus are composed almost entirely of sterile males. They have reduced jaws and a pointed proboscis (nasute), used to squirt a sticky defence compound. Reproductives in a colony consist of at least one king and queen that produce the other castes. Many species of *Nasutitermes* build arboreal carton nests composed of wood, salivary, and faecal fluids (Thorne *et al.*, 1996) and are strictly xylophagous (Martius, 1994).

Termite productivity on St John, U.S. Virgin Islands was examined from two perspectives, the level of the population, and the level of the colony. The hypothesis that termite population density (nest volume) increases with wood resources was tested across four habitats. In addition, a long-term (5 year) observational study of individual colonies was conducted in these habitats. It was hypothesised that growth, reproduction, and survival of colonies would differ among habitats in a way that was predictable from available wood resources.

Methods

Study area

The island of St John, U.S. Virgin Islands, is 53 km² in area, of which two-thirds is a U.S. National Park. Gibney *et al.* (2000) developed a GIS database of St John, describing numerous habitats, of which four of these together cover > 80% of the island: (a) moist forests – found primarily in the higher elevations of the island, and characterised by tropical and subtropical seasonal evergreen trees; (b) dry forests – found at lower elevations, where the range of precipitation is 850–1100 mm per year; (c) woodlands – characterised by an open canopy, and found in pockets near the shoreline; and (d) sparse vegetation – characterised by < 10% vegetative cover, and found along beaches. These habitats are scattered across the island in small patches or in larger patches, of which only small portions are accessible.

Accessible areas were used for individual level measurements (life-history traits) and/or population level measurements (wood density and termite nest volume). All but three areas used for population-level measurements were also used for individual-level measurements. Patches used for individual-level measurements were pooled by habitat type.

Estimation of lying dead wood

Belt transects (10 m × 50 m) were used to estimate the volume of lying dead wood in the four habitats ($n = 6$ per habitat, except for sparse vegetation, $n = 5$). All transects were located at least ≈ 500 m from each other. Wood was sampled using a modification of Eggleton's line intersection method (Eggleton *et al.*, 1996): small wood (diameter < 10 cm) was sampled at 10 m intervals (five sub-samples per transect) on each transect using a randomly oriented line of 1 m extending 0.5 m on either side of the transect. The volume of all small wood touching the line was measured. Similarly, large wood (diameter > 10 cm) was sampled at 10-m intervals along the transect using a randomly oriented line of 10 m, extending 5 m on either side of the transect. Abe (1980) demonstrated that wood attacked by termites maintained its original shape almost intact. Lying dead wood in the study was generally cylindrical in shape. Thus, length and diameter was used to estimate the cylindrical volume of all logs touching the line.

Estimation of *Nasutitermes acajutlae* nest density

Termite nest density was estimated using GPS (Global Positioning System) quadrats at the site of each belt transect; however, GPS quadrats were much larger ($1224.7 \pm 1081.5 \text{ m}^2$). Different habitats were sampled by taking GPS readings at four corners of a (approximately) rectangular shape. The area within the four points of a quadrat was calculated using the methods of De Berg *et al.* (2000). The area lying within the quadrat was thoroughly searched for termite nests. To calculate nest volume of accessible nests the methods of Levings and Adams (1984) were used; three perpendicular diameters of the nest carton were measured using a tree caliper and the nest volume was calculated based on the volume of an ellipsoid ($\frac{4}{3} \times \pi \times r_1 \times r_2 \times r_3$). For inaccessible nests (32 out of 61 nests), nest sizes were classified into three categories (small, medium, and large) and assigned a biomass based on the median value of measured nests in these size classes (small = 120 litres based on 22 measured nests, medium = 245 litres, 24 measured nests, and large = 420 litres, 13 measured nests).

Long-term estimation of population parameters

This portion of the study began in June/July of 1998. Each colony encountered was marked with a metal tree

tag for future identification. Colonies were considered to be reproductively active if core samples (taken with a 1.9 cm diameter soil sampler) contained nymphs in any instar or alates. In 2002, it was recorded whether the reproductives were nymphs or alates. Termite activity in core samples and/or activity in foraging trails directly under nests was used to determine whether colonies were alive. Nest volume of each accessible nests encountered was estimated according to the methods of Levings and Adams (1984) (see above). During subsequent visits in June/July of 2000, 2001, and 2002, colonies were re-measured and re-examined for alates. In addition, survival was assessed in 2003. Colony growth was calculated by subtracting year 1 size from year 2 size except during the first interval of the study. Because there was a 2-year interval between visits (1998–2000), growth was divided by 2 for analyses. Finally, new nests that were encountered were marked when the size of monitored areas was expanded. Most marked colonies were assessed yearly except a few colonies that were not possible to find in 2000. Finally, some nest cartons were too high to assess for reproduction, and others were also too high to measure. These high nests were only used to estimate termite nest density and survival in different habitats.

Projected long-term alate production

The average number of alates produced over a 10-year period by colonies in different habitats was projected using an analysis based on standard life tables (Krebs, 2001; Fuller *et al.*, 2004); however, nest volume was used instead of age because survival and reproduction in nasutes have been shown to be size dependent (e.g. this study, Thorne, 1983; Thorne & Haverty, 2000). Data generated from long-term observations for size-specific probabilities of survival and alate production were used. The number of alates produced in the study was not measured; however, Thorne (1983) found that alate production increased with colony size in *N. corniger*, with a slope of 0.12. Therefore, two sets of curves were generated. In the first, it was assumed that the smallest colony to produce alates produces N alates per year and that alate production does not increase with colony size; in the second, it was assumed that the smallest colony to produce alates also produces N alates per year, but that yearly alate number increases with a slope of 0.12. Growth was not incorporated into the life tables because growth measured in the study did not differ significantly from zero (see below).

Statistics

Comparisons involving termite nest volume and wood volume

A square root transformation for both wood and nest volumes was used to normalise data (Zar, 1984). ANCOVA was used to examine the effects of habitat and volume of lying dead wood on termite nest density simultaneously and

a multiple contrasts test to determine differences among adjusted habitat means.

Comparisons of the relationship between habitat and colony fitness

Nest size, growth, alate production, and survival may be interrelated in *N. acajutlae* (Thorne & Haverty, 2000). Therefore preliminary analyses were conducted, pooling across habitat, to determine which variables to include in final models. To allow the largest sample size possible for each analysis, first the relationship between year, nest volume, and each variable (survival, growth, and alate production) was examined separately. The 1998–2000 interval was excluded from survival analyses; colony growth was divided during this time period by 2 for purposes of comparison with 1-year time intervals. Growth was not significantly related to initial nest volume ($F_{2,98} = 1.64$, $P > 0.35$) or year ($F_{2,98} = 1.64$, $P = 0.20$). It was found that square-root transformed nest volume but not year was significantly related to survival ($F_{\text{nestvol}} = 5.90$, $P = 0.02$, d.f. = 1,125; $F_{\text{year}} = 0.18$, d.f. = 2,125, $P > 0.8$) and alate production ($F_{\text{nestvol}} = 15.45$, d.f. = 1,172, $P < 0.001$; $F_{\text{year}} = 1.49$, d.f. = 3,172, $P > 0.20$). Next the relationship between alate production, colony size and year, and survival until the following year was examined. Only nest volume was a significant predictor of survival ($F_{\text{nestvol}} = 7.70$, d.f. = 1,142, $P < 0.01$; $F_{\text{alate}} = 1.14$, d.f. = 1,142, $P > 0.24$; $F_{\text{year}} = 0.61$, d.f. = 2,142, $P > 0.50$).

For final models of fitness parameters, i.e. those including habitat, it would be possible to include all variables in one large model. However, the sample size varied for each variable because nest size and alate production required one year of data, survival required two consecutive years, and growth required two consecutive years in which a colony was alive. Therefore each dependent variable was examined separately. The relationship between habitat and survival and between habitat and the presence of alates was examined using logistic regression; square-root transformed nest volume was the covariate in these models. The relationship between habitat and nest size and habitat and growth was examined using ANOVA. Finally, termite colonies were visited each year, therefore there is one record for each colony, in each year of the study; however, each colony was included only once in analyses of alate production, growth, and nest size to avoid pseudoreplication. Which year to include each colony was determined randomly.

All tests were run with an α level of 0.05 using SAS (SAS Institute, 1999) or SYSTAT software (Wilkinson, 1998).

Results

Dead wood volume among habitats

Total wood volume differed significantly among habitats (ANOVA, $F_{3,19} = 3.64$, $P = 0.032$). Tukey's HSD test

indicated that dry forests had significantly less total lying dead wood than the other three habitats ($P < 0.05$) (Table 1). Similarly, there were significant differences in the volume of large wood among habitats ($F_{3,19} = 3.65$, $P = 0.031$) and Tukey's HSD test showed that dry forests had significantly less large wood than woodlands ($P < 0.05$) (Table 1). Although dry forests also had the lowest volume of small wood among habitats, these differences were not significant ($F_{3,19} = 2.06$, $P = 0.140$) (Table 1).

Relationship between wood volume and termite nest volume

The interaction term for the initial ANCOVA model (effect of wood volume and habitat on termite nest density) was not significant ($F_{\text{wood} \times \text{habitat}} = 0.171$, d.f. = 7,15, $P = 0.915$), indicating parallel slopes of regression equations for the density of wood volume in each habitat. Therefore, the interaction term was removed from the model. Termite nest volume varied significantly with wood volume ($F_{\text{wood}} = 66.412$, d.f. = 1,21, $P < 0.0001$; Fig. 1). In addition, termite nest volume varied with habitat ($F_{\text{habitat}} = 13.492$, d.f. = 3,19, $P < 0.0001$; Table 1 shows the adjusted mean termite nest volume, i.e. after the effects of wood volume are removed). *Post hoc* tests indicated that termite nest volume in woodlands was significantly higher than in sparse vegetation ($P < 0.0001$) per unit of wood.

Fitness parameters

Individual colonies differed significantly in size among habitats ($F_{3,92} = 5.27$, $P = 0.002$; Table 2) and Tukey's HSD test indicated that nests in sparse vegetation were significantly smaller than those in the other three habitats ($P < 0.01$). There were no significant differences in yearly growth of colonies among habitats ($F_{3,52} = 1.65$, $P = 0.19$; Table 2), and pooled growth across habitats did not differ significantly from 0 (mean \pm SE = 5.40 ± 8.66 litres year⁻¹, $t_{57} = 0.624$, $P > 0.5$). Yearly survival differed significantly among habitats ($\chi^2_3 = 7.88$, $P < 0.05$; Table 2). When the table was collapsed to a comparison between sparse vegeta-

tion and the other three habitats pooled, the differences were also significant ($\chi^2_1 = 6.90$, $P < 0.01$); however, when colony size was included in a logistic regression model, only colony size was significantly related to survival ($F_{\text{nestvol}} = 12.56$, d.f. = 1,147, $P < 0.001$; $F_{\text{habitat}} = 0.92$, d.f. = 3,147, $P = 0.17$). Reproduction also differed significantly among habitats when nest size was taken into account ($F_{\text{alate-vol interaction}} = 2.72$, d.f. = 3,76, $P = 0.05$; $F_{\text{alate}} = 3.2$, d.f. = 3,76, $P = 0.03$). Further analysis of reproduction demonstrated that colonies in sparse vegetation were most likely to produce reproductives at a small size and the probability of reproduction decreased with size; colonies in all other habitats increased alate production with colony size (likelihood ratio $\chi^2_3 = 16.14$, $P = 0.001$; Table 3, Fig. 2). In 2002, 65.8% (25 of 38) of reproductive colonies contained alates or both nymphs and alates. However, the proportion of colonies with alates differed significantly among habitats ($\chi^2_3 = 9.92$, $P < 0.025$; Table 2) reproductive colonies in sparse vegetation were least likely to have alates.

Projected long-term alate production

Figure 2 shows that, within the framework of the assumptions, alate production in sparse vegetation is always lower than alate production in the other habitats, regardless of whether there is a size advantage (i.e. larger colonies produce more alates). See Table 3 for parameters used to generate the curves.

Discussion

The main objective of this study was to examine the association between the nest volume and life-history characteristics of *N. acajutlae*, and the amount of lying dead wood. Results suggest that a population-level parameter (termite nest volume) was positively correlated to dead wood volume (Fig. 1); however, termite nest volume per habitat did not correlate with the fitness of individual colonies (Table 2).

Table 1. Mean (SE, *n*) values for habitat parameters measured in the four habitats.

	Dry	Moist	Sparse	Woodland
Total wood volume (litres per 500 m ²)	14.96* (19.56, 6)	358.63 (384.41, 6)	470.37 (372.17, 5)	765.58 (971.98, 6)
Large wood volume (litres per 500 m ²)	13.87* (19.7, 6)	354.81 (380.5, 6)	452.7 (354.94, 5)	749.09 (966.69, 6)
Small wood volume (litres per 500 m ²)	1.09 (0.94, 6)	3.81 (4.53, 6)	17.66 (31.74, 5)	16.48 (14.54, 6)
Adjusted means termite nest volume (litres per m ²)	1.090 (0.06, 6)	1.056 (0.05, 6)	1.167 (0.05, 5)	1.504* (0.05, 6)
Number of nests per hectare	0.17 (0.18, 6)	0.42 (0.49, 6)	0.72 (0.62, 5)	0.55 (0.43, 6)

*Significantly different $P < 0.05$.

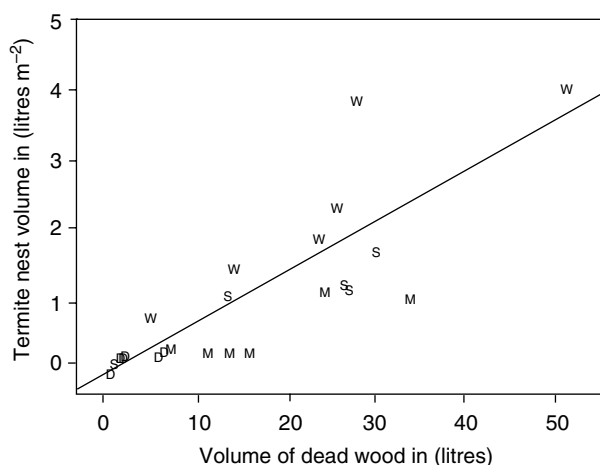


Fig. 1. Relationship between square-root transformed volume of lying dead wood (measured using belt transects in 2001) and termite nest volume (measured using GPS quadrats in 2002). Regression equation: Nest volume = $-0.0156 + 0.0728 \text{ wood}$; $n = 23$; $r^2 = 0.689$; $P < 0.0001$. D = Dry forests, M = moist forest, S = sparse vegetation, and W = woodland.

The correlation between termite nest volume and volume of lying dead wood across all four habitats suggests that resource availability and intraspecific competition plays an important role in controlling termite populations. It was also found that woodlands had more termites per unit wood than the other three habitats. These differences could be due to a number of factors including variation in wood quality (Takamura, 2001), interspecific competition (Korb & Linsenmair, 2001), and predation (Korb & Linsenmair, 2002). Currently, no data are available to distinguish between these possibilities. Overall, woodlands had both the highest wood volume and termite nest volume, while moist forests and sparse vegetation were intermediate for both parameters. Thus, the population-level observations suggest that dry forests are the least and woodlands the most productive habitats for *N. acajutlae*.

It seems likely that habitats differ in wood density because they differ in both the input of dead wood from resident trees and from outside (allochthonous) sources. Moist forests appeared to have higher biomass of living

trees compared with the other three habitat types, therefore may also contribute more dead wood, followed by dry forests, sparse vegetation and woodlands (P.D. Jeyasingh pers. obs.; Gibney *et al.*, 2000). However, woodlands and sparse vegetation may receive allochthonous inputs of dead wood from other habitats because of their location on the island. During storms, dead wood may be flushed from high elevation moist forests to lower elevation valley habitats such as woodlands and sparse vegetation. Sparse vegetation is located along shores, thus probably receives driftwood, particularly after storms. Although dry forests are found at lower elevations, they are not located at the bottom of the valleys or along shorelines and hence may not receive extra-neous dead wood during storms.

In contrast to population-level observations, the observations of individual colonies indicated that colonies inhabiting sparse vegetation were significantly less fit than colonies in the other habitats. First, the probability of survival increased with colony size in all habitats. Because colonies in sparse vegetation were smaller, they had higher mortality on average than colonies in the other habitats. Second, the probability of alate production in sparse vegetation decreased with size, but increased in the other habitats. Third, fewer of the colonies with reproductives in sparse vegetation had fully developed alates. Although alates were not counted, it seems likely that the number of alates produced also differed. Finally, the life table analyses suggest that colonies in sparse vegetation could have substantially lower alate production over a 10-year period than colonies in the other habitats, whether or not alate production increases with size (Fig. 2). Thus, unlike termite productivity at the level of the habitat, individual colonies in sparse vegetation seem to have the lowest fitness. The data in Table 2 suggest that colonies in moist forests may have the highest and colonies in dry forests and woodlands intermediate fitness.

The discrepancy between population-level and individual-level results may be due to the predictability of wood resources. Life-history theory suggests that individuals in unpredictable environments reproduce earlier than individuals in more stable environments (Stearns, 1992). Because sparse vegetation occurs along shorelines, input of allochthonous wood may be particularly important. If this input is mainly due to storms, it may be particularly

Table 2. Mean values for individual nest fitness parameters measured in the four habitats.

	Dry	Moist	Sparse	Woodland
Nest volume (litres)	208.5	313.1	136.6*	204.2
(SE, <i>n</i>)	(36, 20)	(41, 13)	(17.2, 30)	(23.2, 33)
Yearly growth (litres)	29.9	5.57	12.22	15.03
(SE, <i>n</i>)	(7.4, 13)	(10.0, 7)	(6.9, 15)	(5.8, 21)
Per cent survival (<i>n</i>)	77.8 (54)	90 (48)	56.5 (55)	75 (75)
Per cent of reproductive colonies with some alates (<i>n</i>)†	100 (8)	85.7 (7)	33.3 (9)	57 (14)

*Significantly different $P < 0.01$ Tukey's HSD test.

† $P < 0.025$, χ^2 contingency analysis.

Table 3. Size distribution of colonies and size-specific alate production and survival rates for colonies in sparse vegetation and the other three habitats pooled.

Size class	Dry, moist and woodland		Sparse vegetation		
	Per cent in size class	Proportion with alates	Per cent in size class	Proportion with alates	Size-specific survival per year
< 50	10.6	0	20	0.14	0.78
50	13.6	0.23	13.3	0.5	0.62
100	10.6	0.36	33.3	0.58	0.8
150	15.2	0.58	13.3	0.5	0.8
200	10.6	0.76	3.3	0.67	0.84
250	12.1	0.86	6.7	0.8	0.97
300	6	0.54	6.7	0.67	0.97
350	12.1	0.93	3.3	1	0.97
450	6	1	–	–	0.97
550	3	0.8	–	–	0.97

unpredictable. In the years preceding 2001 (when dead wood volume was quantified), there were frequent hurricanes in the vicinity of St John: including 1995 (Marilyn), 1996 (Bertha), 1998 (Georges), 1999 (Lenny), and 2000 (Debby). Storms may provide large amounts of wood that allow numerous new colonies to form. Colonies may grow quickly, use up the resources, and die out. Consistent with this prediction, it was found that sparse vegetation plots had significantly smaller colonies (Table 2) at higher population densities (colonies per ha), although the differences in density were not significant (Table 1).

Apart from unpredictable food supply, other habitat-specific factors may have caused the observed variation in life history and nest volume of *N. acajutlae* colonies in sparse vegetation. Takamura (2001) reported higher decomposition rates (by termites) in a light hardwood tree (*Shorea*

macroptera) compared with a hardwood tree (*Neobalanocarpus heimii*). The C:N ratio of light hardwood is much lower than heavy hardwood, indicating that nitrogen content in wood may affect the efficiency of termites to decompose wood. Secondary metabolites in wood also differ among tree species. Tree species composition differed among the four habitats studied (Gibney *et al.*, 2000). In particular, sparse vegetation was dominated by salt-tolerant trees (e.g. sea grape, *Coccoloba uvifera*), and could potentially differ in their chemical composition. Therefore, the potential role of wood *quality* (both C:N ratio and secondary metabolites) in limiting termite populations warrants further investigation. A few studies demonstrate the importance of humidity (e.g. Rudolph *et al.*, 1990) and temperature (Korb & Linsenmair, 1998) on termite colonies. These factors probably vary among habitats on St John (C. A. Fuller, pers. obs.); however, their effect on *N. acajutlae* nest volume remains to be tested. Studies on the spatial distribution of termites have highlighted the importance of inter- and intraspecific competition (Levings & Adams, 1984; Lepage *et al.*, 1995; Crist, 1998; Buschini, 1999; Korb & Linsenmair, 2001) in structuring termite populations. Although there are no other species of arboreal nesting termites known on St John (Jones & Nalepa, 2002), competition with fungi (Holt, 1987, 1990), and other macro-detritivores (Korb & Linsenmair, 2001) could be a major factor in controlling the abundance and distribution of *N. acajutlae* populations in different habitats. The absence of inter-colonial agonism between *N. acajutlae* colonies on St John (Fuller *et al.*, 2004) suggests that intra-specific competition may not be severe.

Predation may also affect termite life history and biomass. Ant predation is recognised as the main cause of nest mortality in termites (Lepage & Darlington, 2000). In the >350 nests monitored over the 4-year period, no evidence of ant predation was found in any of the four habitats. Although anole lizards were observed preying on *N. acajutlae* workers, anole predation was significantly higher in dry forests (P. D. Jeyasingh, unpubl. data), and not in sparse vegetation. Therefore, predation may not be

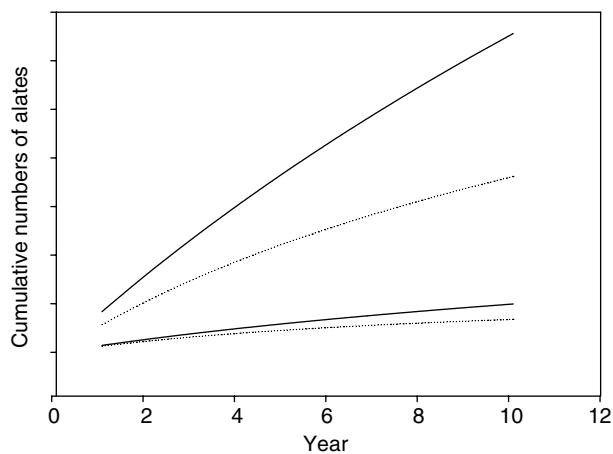


Fig. 2. Projected alate numbers produced by an average colony in sparse vegetation (solid lines) and the other three habitats pooled (dashed lines) over a 10-year period. The bottom two lines represent the case when there is no size advantage to alate production. The upper two lines represent a scenario in which alate production increases with size (slope = 0.12; *sensu* Thorne, 1983).

an important factor in regulating the observed variation in nest volume and life-history strategy of established colonies in sparse vegetation; however, the predator–prey interactions affecting termites are poorly understood (Lepage & Darlington, 2000), and these observations warrant further research.

Although many studies document the density and distribution patterns of nasutes (e.g. Thorne & Haverty, 2000), it is believed that this study is the first to document habitat-specific variation in life-history characteristics of individual nasute colonies. In their study on African mound-building termite *Macrotermes bellicosus*, Korb and Linsenmair (1999) conclude that forests are sub-optimal habitats based on computer simulated lifetime reproductive success (LRS) data. The results from the work reported here from population-level (nest volume) and individual-level (fitness) studies indicate different optimal habitats. Although dry forests had the lowest volume of dead wood and termite nest volume, colonies therein were larger, less likely to reproduce, and had higher survival compared with colonies in sparse vegetation. Therefore, from a population perspective, sparse vegetation is capable of supporting more *N. acajutlae* colonies. However, from an individual perspective, colonies in sparse vegetation had lower fitness; therefore, sparse vegetation is not an optimal habitat for individual *N. acajutlae* colonies. These opposing habitat-specific effects on different levels of *N. acajutlae* organisation (individual and population level) suggest that termite population studies should include individual (colony) life-history parameters into analysis and conclusions.

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References

- Abe, T. (1980) Studies on the distribution and ecological role of termites in a lowland rain forest of West Malaysia. The role of termites in the process of wood decomposition in Pasho Forest Reserve. *Revue Ecologie et Biologie du Sol*, **17**, 23–40.
- Abe, T. (1987) Evolution of life types in termites. *Evolution, Coadaptation and Biotic Communities* (ed. by S. Kawano, J. H. Connell and T. Hidaka), pp. 128–148. University of Tokyo Press, Tokyo.
- Bignell, D.E. & Eggleton, P. (2000) Termites in ecosystems. *Termites: Evolution, Sociality, Symbiosis, Ecology* (ed. by T. Abe, D. E. Bignell and M. Higashi), pp. 363–408. Kluwer, Dordrecht.
- Buschini, M.L.T. (1999) Spatial distribution of nests of *Nasutitermes* sp. (Isoptera: Termitidae) in a Cerrado Area in South-eastern Brazil. *Environmental Entomology*, **28**, 618–621.
- Constantino, R. (1992) Abundance and diversity of termites (Insecta: Isoptera) in two sites of primary rain forest in Brazilian Amazonia. *Biotropica*, **24**, 420–430.
- Crist, T.O. (1998) The spatial distribution of termites in shortgrass steppe: a geostatistical approach. *Oecologia*, **114**, 410–416.
- De Berg, M., van Kreveld, M., Overmars, M. & Schwarzkopf, O. (2000) *Computational Geometry, Algorithms and Applications*, 2nd rev. edn, p. 367. Springer, New York.
- Eggleton, P. (2000) Global patterns of termite diversity. *Termites: Evolution, Sociality, Symbiosis, Ecology* (ed. by T. Abe, D. E. Bignell and M. Higashi), pp. 25–52. Kluwer, Dordrecht.
- Eggleton, P., Bignell, D.E., Sands, W.A., Mawdsley, N.A., Lawton, J.H., Wood, T.G. *et al.* (1996) The diversity, abundance, and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of the Royal Society of London*, **B 351**, 51–68.
- Facelli, J.M. & Pickett, S.T.A. (1991) Plant litter – its dynamics and effects on plant community structure. *Botanical Review*, **57**, 1–32.
- Fuller, C.A., Jeyasingh, P.D. & Harris, L.W. (2004) Lack of agonism in an insular Carribean termite, *Nasutitermes acajutlae*. *Journal of Insect Behaviour*, **17**, in press.
- Fuller, C.A. & Jeyasingh, P.D. (2004) Acanthocephalan (Oligacanthorhynchidae) parasitism of the Caribbean termite *Nasutitermes acajutlae*: implications for reproductive success. *Insectes Sociaux*, **51**, in press.
- Gibney, E., Thomas, T., O'Reilly, R. & Devine, B. (2000) *The US Virgin Islands Vegetation Classification System*. Conservation Data Center Publication, p. 24. University of the Virgin Islands, St Thomas, USVI.
- Holt, J.A. (1987) Carbon mineralization in semi-arid northern Australia: the role of termites. *Journal of Tropical Ecology*, **3**, 255–263.
- Holt, J.A. (1990) Carbon mineralization in semi-arid tropical Australia: the role of mound building termites. *Australian Journal of Ecology*, **15**, 133–134.
- Jones, S.C. & Nalepa, C.A. (2002) Survey of the termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of St. John, U.S. Virgin Islands. *Sociobiology*, **39**, 155–163.
- Korb, J. & Linsenmair, K.E. (1998) The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* mounds in different habitats of a West African Guinea savanna. *Insectes Sociaux*, **45**, 51–65.
- Korb, J. & Linsenmair, K.E. (1999) Reproductive success of *Macrotermes bellicosus* (Isoptera: Macrotermitinae) in two neighboring habitats. *Oecologia*, **118**, 183–191.
- Korb, J. & Linsenmair, K.E. (2001) Resource availability and distribution patterns, indicators of competition between *Macrotermes bellicosus* and other macro-detritivores in the Comoe National Park, Cote d'Ivoire. *African Journal of Ecology*, **39**, 257–265.
- Korb, J. & Linsenmair, K.E. (2002) Evaluation of predation risk in the collectively foraging termite *Macrotermes bellicosus*. *Insectes Sociaux*, **49**, 264–269.
- Krebs, C.J. (2001) *Ecology: the Experimental Analysis of Distribution and Abundance*. Benjamin Cummings, San Francisco.

- Lepage, M. & Darlington, J.P.E.C. (2000) Population dynamics of termites. *Termites: Evolution, Sociality, Symbiosis, Ecology* (ed. by T. Abe, D. E. Bignell and M. Higashi), pp. 333–362. Kluwer, Dordrecht.
- Leponce, M., Roisin, Y. & Pasteels, J.M. (1995) Environmental influences on the arboreal nesting termite community in New Guinean coconut plantations. *Environmental Entomology*, **24**, 1442–1452.
- Levings, S.C. & Adams, E.S. (1984) Intra- and inter-specific territoriality in *Nasutitermes* (Isoptera: Termitidae) in a Panamanian mangrove forest. *Journal of Animal Ecology*, **53**, 705–714.
- Martius, C. (1994) Diversity and ecology of termites in Amazonian forests. *Pedobiologia*, **38**, 407–428.
- McSorley, R. (1997) Relationship of crop and rainfall to soil nematode community structure in perennial agroecosystems. *Applied Soil Ecology*, **6**, 147–159.
- Mikola, J., Yeates, G.W., Wardle, D.A., Baker, G.M. & Bonner, K.I. (2001) Response of soil food-web structure to defoliation of different plant species combinations in an experimental grassland community. *Soil Biology and Biochemistry*, **33**, 205–214.
- Nalepa, C.A. (1990) Life history characteristics associated with a wood diet and the evolution of termite eusociality. *Social Insects and the Environment* (ed. by G. K. Veeresh, B. Malik and C. A. Virakmath), pp. 643–644. Oxford & IBH, Bangalore.
- Roisin, Y. & Pasteels, J.M. (1986) Differentiation of worker-derived intercastes and precocious imagoes after queen removal in the neo-Guinean termite *Nasutitermes principis* (Desneux). *Journal of Morphology*, **189**, 281–293.
- Rudolph, D., Glocke, B. & Rathenow, S. (1990) On the role of different humidity parameters for the survival, distribution and ecology of various termite species. *Sociobiology*, **17**, 129–140.
- SAS Institute (1999) SAS. *Version 8*. SAS Institute Inc., Cary, North Carolina.
- Scholwaller, T.D. (1994) Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following hurricane Hugo. *Biotropica*, **26**, 312–319.
- Stearns, S.C. (1992) *The Evolution of Life Histories*, p. 249. Oxford University Press, Oxford.
- Takamura, K. (2001) Effects of termite exclusion on decay of heavy and light hardwood in a tropical rain forest of peninsular Malaysia. *Journal of Tropical Ecology*, **17**, 541–548.
- Thorne, B.L. (1983) Alate production and sex ratio of the neotropical termite *Nasutitermes corniger* (Isoptera; Termitidae). *Oecologia*, **58**, 103–109.
- Thorne, B.L. (1985) Numerical and biomass caste proportions in colonies of the termites *Nasutitermes corniger* and *N. ephratae* (Isoptera: Termitidae). *Insectes Sociaux*, **32**, 411–426.
- Thorne, B.L., Collins, M.S. & Bjorndal, K.A. (1996) Architecture and nutrient analysis of arboreal carton nests of two neotropical *Nasutitermes* species (Isoptera: Termitidae), with notes on embedded nodules. *Florida Entomologist*, **79**, 27–37.
- Thorne, B.L. & Haverty, M.I. (2000) Nest growth and survivorship in three species of neotropical *Nasutitermes* (Isoptera: Termitidae). *Environmental Entomology*, **29**, 256–264.
- Wilkinson, L. (1998) *SYSTAT: the System for Statistics*. SYSTAT Inc., Evanston, Illinois.
- Wood, T.G. & Sands, W.A. (1978) The role of termites in ecosystems. *Production Ecology of Ants and Termites* (ed. by M. V. Brian), pp. 245–292. Cambridge University Press, Cambridge.
- Zar, J.H. (1984) *Biostatistical Analysis*, 4th edn, p. 275. Prentice Hall, Englewood Cliffs, New Jersey.

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