Nest Growth and Survivorship in Three Species of Neotropical *Nasutitermes* (Isoptera: Termitidae)

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ABSTRACT Long-term growth and survivorship of individual arboreal nests were studied in three species of Neotropical termites in the genus *Nasutitermes.* Of the 29 *N. corniger* (Motschulsky) and seven *N. ephratae* (Holmgren) nests monitored in an area of young second-growth in Panama, 12 (41%) *N. corniger* and four (57%) *N. ephratae* nests remained active throughout the 9- to 11-mo study. There was no significant difference in survivorship between small and large nests of either species. In surviving *N. corniger* nests with a single queen, the net increase in volume was highly correlated ($r = 0.87$, $n = 9$) with queen wet weight. There was a marked seasonality to nest expansion in both *N. corniger* and *N. ephratae,* with growth occurring almost exclusively during the wet season. Seventeen *N. acajutlae* (Holmgren) nests were monitored for 4–9 yr on Guana Island, British Virgin Islands. Four of the 17 (23.5%) *N. acajutlae* nests survived the study period, and two more abandoned their original nest and relocated. Within this limited sample of colonies, *N. acajutlae* nests that were large (>150,000 cm^3) at the beginning of the study had a higher probability of survival than did small (<100,000 cm^3) nests. Nest budding, relocation, and resprouting are mechanisms that *Nasutitermes* may use to create a new nest for all or a portion of an established colony. The ontogeny of incipient *Nasutitermes* colonies is discussed as a sequence in which a young colony remains cryptic within wood, building its population size to a point where the colony can maintain and defend a nest. Early in a wet season, termites then venture from within wood to build and occupy a small arboreal nest.

KEY WORDS *Nasutitermes acajutlae, Nasutitermes corniger, Nasutitermes ephratae,* termite colony survivorship, termite colony longevity, arboreal nests

THE TROPICOPOLITAN TERMITE genus *Nasutitermes* (Termitidae: Nasutitermitinae) is the most speciose of all isopteran genera, containing 74 described species from the Neotropics alone (Constantino 1998). Unlike most termites, many species of *Nasutitermes* build arboreal carton nests composed of masticated wood and occasionally other materials such as sand cemented together with salivary and fecal fluids (Light 1933, Emerson 1938, Thorne et al. 1996a). The majority of nest-building termites construct mounds on the ground, but nesting in trees has enabled species of *Nasutitermes* and several other genera to colonize and exploit a new habitat (Emerson 1938, Noirot 1970).

Nasutitermes nests are built on the trunk or on or around a branch of a host tree. Typically, the termites build a network of trails or "galleries" from the nest to other regions of the tree, down the trunk (sometimes within the trunk), or along the underside of branches to connect the nest with other food sources in the area. *Nasutitermes* nests reach enormous sizes in some species, occasionally exceeding 2 m in height (e.g., *N. acajutlae* Collins et al. 1997; Haverty et al. 1997; *N. rippertii* (Rambur) R. H. Scheffrahn, personal communication). In all species of arboreal *Nasutitermes,* nests are built with reinforced, dense zones of carton that act to protect at least the queen cell from vertebrate predators, damage from a falling branch, or toppling of the nest by a storm or decay of its host tree (e.g., Hubbard 1877, Andrews 1911, Emerson 1938, Thorne 1980, Lubin and Montgomery 1981). These termite nests thus represent the focal reproductive location for the colony, the hub of its foraging network, and a substantial investment of time and energy in construction and maintenance.

In this article we report on long-term studies of arboreal nest growth and survivorship in three species of Neotropical *Nasutitermes.* "Nest growth" refers to the expansion of their carton nest by the termites housed within; "nest survivorship" means survivorship of the termite colony, or portion of the colony, active within the nest. Twenty nine nests of *N. corniger* (Motschulsky) and seven nests of *N. ephratae* (Holmgren) were followed for 9–11 mo in Panama, and 17 nests of *N. acajutlae* (Holmgren) were monitored for 4–9 yr on Guana Island, British Virgin Islands. We tested the null hypothesis that colonies in large and small nests have an equal probability of survival, even though larger nests have a greater volume and physical structure to protect them from injury or disturbance, and they have already survived through the early age classes. The processes of incipient nest formation and relocation of established nests are also discussed.

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Materials and Methods

Study Area. All of the individual *N. corniger* ($n = 29$) and *N. ephratae* ($n = 7$) nests monitored in Panama were located in an area of young second-growth that had been burned 3–6 yr previously, with only small trees left standing, near Frijoles, a settlement on the south shore of the Panama Canal, Panama (9° 09′ N, 79° 51′ W) (Thorne 1983). Every arboreal nest within that region of second-growth was included in the study. All nests were located within a radius of 0.5 km. The *N. acajutlae* nests ($n = 17$) were on or near the flats of White Bay Beach of Guana Island, a small (340 ha; highest peak 246 m), but biologically diverse, reserve in the British Virgin Islands (Lazell 1996). The majority of *N. acajutlae* nests on the White Bay Beach flats were part of the study; however not every nest in the area was included because some were too high in the canopy to measure accurately. In the Panama site by agreement with the landowner, and on Guana Island because it is managed as a conservation area, all nests were left undisturbed by humans during the course of the study.

Nest Measurements. All individual nests included in this study were accessible by standing or climbing. Measurements of the hemiaxes (height, width, and depth) were taken with a measuring tape and recorded on each monitoring date. The position of these measurements was generally at the maximum dimension of height, width, or depth, although if the nest had an exaggerated protrusion that compromised the typically ellipsoidal shape (irregularities most likely to occur in *N. corniger*), account was taken and the recorded measurement was the best fit to a more regular ellipsoid. Nest volumes (cm^3) were estimated as the volume of an ellipsoid ($4/3\ \pi$ a b c, where a, b, and c are lengths of the hemiaxes) (Thorne 1980, 1983, 1984, 1985; Levings and Adams 1984; Leponce et al. 1995). [Note that Weigert (1970) and Weigert and Coleman (1970) used nest length × width × height as an index of arboreal *Nasutitermes* nest volume, and Clarke (1993) used the maximum perimeter of arboreal *Nasutitermes* as a volumetric correlate]. In Panama, portions of all host tree trunks or branches encased by the nest were measured. Their volumes were calculated as cylinders, and subtracted from the total nest volume measurement to yield the volume of the nest carton. On Guana Island the *N. acajutlae* nests were built on substantially larger trees (often on mature sea grape, *Coccoloba uvifera;* Polygonaceae), and were typically perched on the trunk, on a branch, or at the junction of the trunk and a branch. Wood from the host tree did penetrate nests, but for practical reasons the volume of enclosed wood could not be measured precisely. Because these *N. acajutlae* nests were much larger than the Panama series in total and in proportion to wood encased by the nest, host tree wood was not measured or subtracted from the calculation of nest volume.

In Panama, nest measurements were taken during the months of May to July 1979, with additional nests added to the study group throughout that time as different areas of the site were explored (two additional nests were added to the study in October 1979). In total, 29 *N. corniger* nests were included in the study, along with seven *N. ephratae* nests within the same site. Further measurements on the Panama nests were taken from October 1979 to January 1980, with the final measurement of surviving nests made on 1 April 1980.

In total, 17 nests of *N. acajutlae* were measured on Guana Island. One was first measured in July 1989, and 11 additional nests were first measured in October 1992. Subsequent measurements were made in October of 1993, 1994, and 1998. An additional nest was added to the study in 1993 and four more nests were added in 1994.

At the same time that individual nests were measured, photographs of each nest were taken from a specific position and orientation and repeated at each monitoring interval to record the nest profile(s). Scale rulers included in the photos could be used subsequently to check measurements, and photos could be compared with document nest growth.

Nest Dissections. Weights of queens in *N. corniger* colonies were determined following complete dissection of the nest and removal of the queen from the royal cell. Entire carton nests were excised from the host trees (wood encompassed by the nest was included in the sample), placed in thick plastic bags, and transported to the Smithsonian Tropical Research Institute's laboratory on Barro Colorado Island, Republic of Panama. Colonies were refrigerated for 24–48 h to inactivate the termites. Nests were then sequentially shaved and shaken over a collection tray, allowing termites to fall from the exposed galleries. Upon location of the royal cell, the sides were scraped carefully to open the royal chamber and collect the queen(s).

Data Analysis. Nest volumes were calculated for each observation and plotted over the entire length of each study to visualize the variation in growth rate for the nests of all three species of *Nasutitermes.* Initial size of nests of *N. corniger* and *N. acajutlae* were stratified into small ($<3{,}000\ cm^3$ and $<100{,}000\ cm^3$, respectively) and large ($>6{,}000\ cm^3$ and $>150{,}000\ cm^3$, respectively) size categories. Survivorship of small and large nests was compared with logistical regression (SAS Institute 1998) and contingency table analysis (Steele and Torre 1960). Chi-square values were tested at the $\alpha = 0.05$ level.

Newly Constructed Nests. Observations on incipient nest formation and on nest relocation were made during the course of the study in both sites. Recognition of these events was possible because of long-term familiarity with established nests, making new nests that appeared during the course of the research available for investigation.

Voucher Specimens. Voucher specimens are deposited in the USNM collection of the Smithsonian Institution.

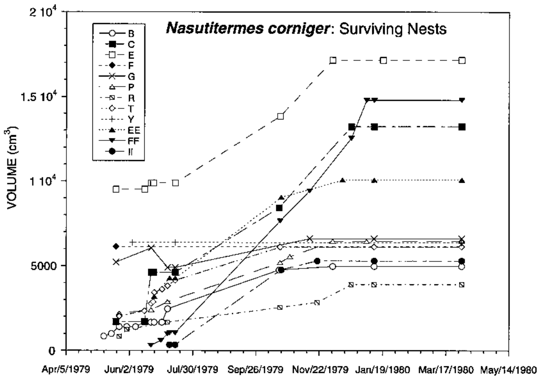

Fig. 1. Growth of *N. corniger* nests that survived throughout the monitoring period. Note consistent lack of growth during the dry season (January through mid-April in 1980). (Figure does not show growth of budded nests.)

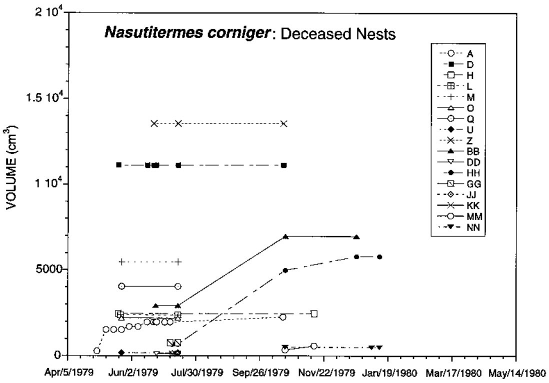

Fig. 3. Growth of *N. corniger* nests that died during the course of the study.

Results

Nest Growth and Survivorship. Of the 29 *N. corniger* nests, 12 (41%) survived the 9–11-mo study period. Of those, only two (17% of the survivors) did not grow at all in external dimensions, but one increased in volume from 296 cm^3 on 22 June 1979 to 14,781 cm^3 on 5 January 1980, a 4,893% increase in volume in just 6.5 mo (Figs. 1 and 2). Thirteen of the 17 *N. corniger* nests that ultimately died during the study (76%) showed no signs of growth even during the period that they remained active (Fig. 3). There was no relationship between nest volume for *N corniger* at the beginning

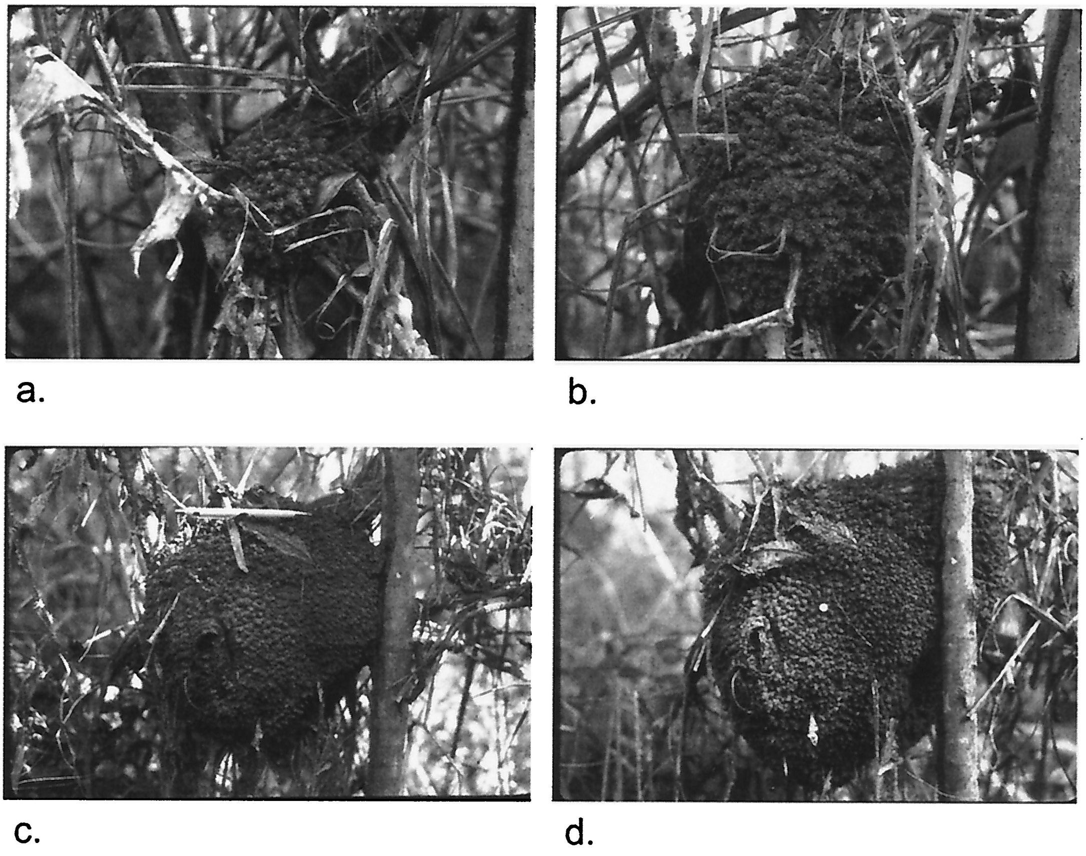

Fig. 2. Growth of *N. corniger* nest FF in Frijoles, Panama, over 5 mo. (a) 22 June 1979. (b) 7 July 1979. (c) 18 October 1979. (d) 14 November 1979.

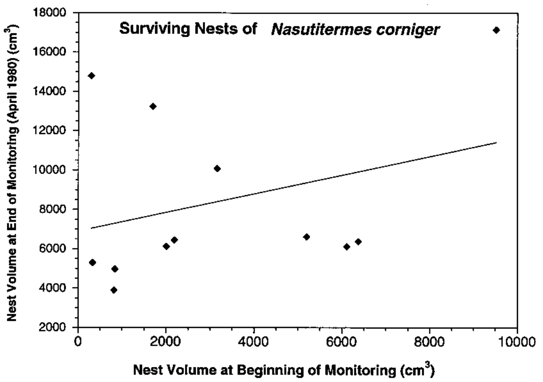

Fig. 4. Relationship between *N. corniger* nest volume at the end of the growth period relative to the initial volume. Data are only from nests that survived the entire study period. The correlation was not significant ($r = 0.32$).

of monitoring and at the end of the monitoring period ($r = 0.32$, $n = 12$) (Fig. 4). Thus, nest size at the beginning of the study was not a good predictor of nest size at the end of the study.

The volume of *N. corniger* nests at the beginning of monitoring (May, June, or July 1979) associated with survivorship to April 1980 is shown in Fig. 5. The two nests for which measurements did not begin until October 1979 (both of which died before April 1980) were not included in this analysis because of a different total monitoring interval. We tried a simple fit using logistical regression and found no significant relationship between initial nest size and survival ($\chi^2 = 0.74$). To test the original hypothesis (Ho: PS = PL, where PS is the probability of survival of small nests, and PL is the probability of survival of large nests), we compared the probability of survival of nests with volumes of <3,000 cm^3 at the beginning of monitoring (PS = 0.375) versus survivorship of nests with a first recorded volume exceeding 6,000 cm^3 (PL = 0.60). There was no significant difference in survivorship over the 9–11-mo period between small and large nests of *N. corniger* ($\chi^2 = 0.86$), leading us to accept the null hypothesis that large and small nests have an equal probability of survival within this population.

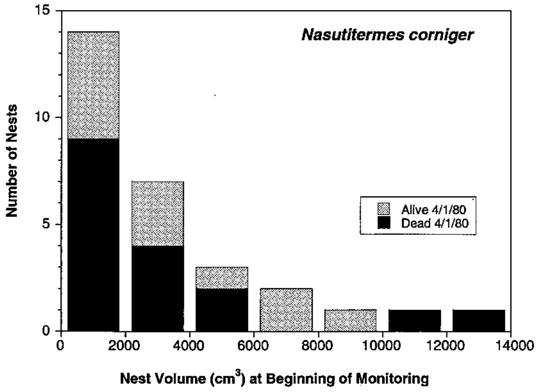

Fig. 5. Survivorship of *N. corniger* nests based on initial size. Monitoring of individual nests began in May, June, or July of 1979.

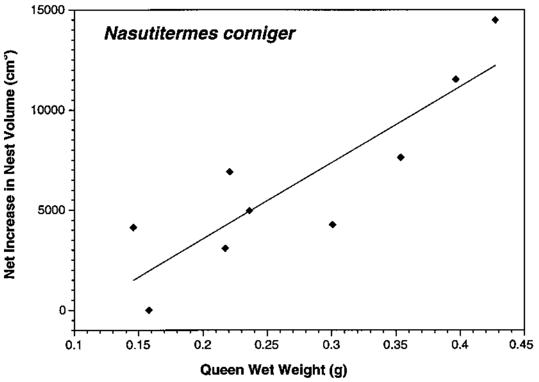

Fig. 6. Relationship between queen wet weight (*N. corniger* colonies with monogynous queens only) and net increase in nest volume during the course of the study. The correlation was highly significant ($r = 0.87$). Monitoring of individual nests began in May, June, or July of 1979. Nests were collected and dissected in April 1980 to expose and measure reproductives.

Another consideration in evaluating growth of *N. corniger* nests is that this species is facultatively polygynous. Because colonies with multiple primary queens grow faster in both population size and nest volume in the early age classes (Thorne 1984, 1985), some of the observed variance in nest growth rates might be explained by queen number. The *N. corniger* nests that survived until April 1980 were collected and all but one (Y) were fully dissected (technique described in Thorne and Noirot 1982). All but two of the nests had a single primary queen; nest G had two queens and nest T contained numerous wingless alates in the queen cell, suggesting that queen replacement was underway. In the monogynous surviving *N. corniger* nests, the net increase in volume from summer 1979 to April 1980 is highly correlated ($r = 0.87$) with queen wet weight at the time of nest dissection (Fig. 6). Notably, several of the nests with the highest growth rates (E, FF, C) also had large queens (>0.35 g). However, nest EE also had a high growth rate, but only a moderately sized monogynous queen (0.22 g) at the time of dissection.

Generalizations about growth rates of *N. ephratae* nests from Frijoles, Panama are risky because of the relatively small number of nests monitored. Four of seven (57%) nests in the study survived the period of the monitoring. The highest growth rate among the survivors was a nest that increased from 1,044 cm^3 on 24 May 1979 to 4,938 cm^3 on 21 November 1979, and then remained at that size through 1 April 1980 (Fig. 7). None of the three nests that ultimately died grew during the study (Fig. 7). One of the four survivors did not increase in size during the monitoring period. The largest *N. ephratae* nest, estimated at 42,272 cm^3 on 24 May 1979, fell to the ground when its host tree, par-

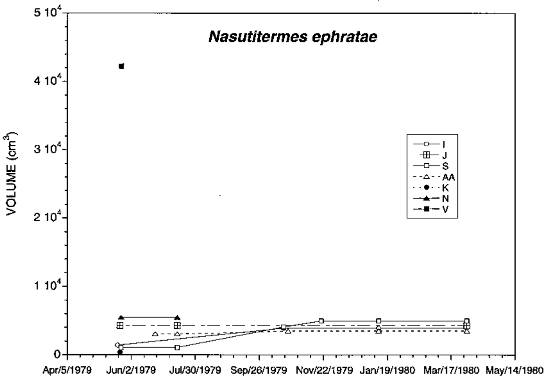

Fig. 7. Growth of *N. ephratae* nests, including survivors (open symbols) and colonies that died (dark symbols) during the course of the study. Note lack of nest expansion during the dry season (January through mid-April in 1980).

Table 1. Volume (cm^3) of nests of *N. acajutlae* on Guana Island, British Virgin Islands, from 1992 to 1998

Colony	Year[b]				
	1992	1993	1994	1996	1998
G1	160,739	186,526	142,424	Relocating	(161,432)[c]
G2[a]	569,185	750,093	902,172		1,281,085
G3	280,730	281,103	288,500		Dead
G4	35,657	Dead			
G5	11,454	23,381	30,192	Dead	
G6	57,738	Dead			
G7	45,629	68,757	87,186	Dead	
G8	9,050	13,205	13,154		Dead
G9	82,491	91,937	Dead		
G10	139,409	208,578	197,072	Dead	
G11	199,444	—	523,421	Relocating	(279,789)[c]
G12	85,790	134,250			287,947
G13		54,629		Dead	
G14			160,896		174,713
G15			66,481		251,963
G16			24,013		Dead
G17			7,830	10,458	Dead

[a] Volume of this colony was 212,171 cm^3 in 1989.

[b] Hurricane Luis damaged buildings on Guana Island in 1995 and limited access to field sites during October, thus no measurements were taken.

[c] These measurements were taken after the colony had relocated.

tially consumed by termites, fell over (event noted and nest dead at 13 July 1979 monitoring). The *N. ephratae* nests that began as the two largest in this study, as well as the smallest nest at the beginning of the project (373 cm^3), died during the course of the research. These trends also suggest acceptance of the original hypothesis (probability of survival is indistinguishable for small and large nests) for *N. ephratae,* although the sample size of seven nests is too small to evaluate with statistical rigor.

There was a marked seasonality to nest expansion in both *N. corniger* and *N. ephratae* (Figs. 1 and 7), with growth usually being limited to the wet season. During the year of the study, the dry season lasted from early January until mid-April 1980. The rare cases in which nest growth did occur over the dry season were in two cases of nest budding in *N. corniger.* Buds had been initiated during the wet season, but there was limited continued growth of the satellite nests during the dry season (budded nests not included in the above data; see below for further discussion of budding).

Nasutitermes acajutlae nests monitored on Guana Island are obviously much larger nests, on average, than for either *N. corniger* or *N. ephratae* at the Panama site (Table 1). *N. acajutlae* characteristically builds larger nests than *N. corniger* or *N. ephratae,* and the habitat for the *N. acajutlae* study was mature vegetation, whereas the Frijoles, Panama, site was young second growth. Of the 17 *N. acajutlae* nests tracked on Guana Island, only four of the 17 (23.5%) survived the duration of monitoring (generally 4–6 yr; 9 yr for a single colony which was a survivor) (Fig. 8). Of the remaining 13 nests, 11 (64.7% of the total) died (Fig. 9), and two (11.8% of the original number) abandoned their original nest and relocated (see below). Including the two relocated but surviving colonies, plus the four nests that remained active during the course of the study, six of the total of 17 colonies (35%), survived the total period of the research. The simple fit using logistical regression revealed no significant linear relationship between initial nest size and survival (χ^2 = 2.47). In contrast with *N. corniger, N. acajutlae* nests that were large at the beginning of monitoring (>150,000 cm^3) had a higher probability of survival than small nests (<100,000 cm^3) (χ^2 = 3.84) (Fig. 10), although we caution that the sample size was limited, particularly among large nests.

New Nests from Old. There are three circumstances in which a new *Nasutitermes* nest can arise from an established nest. Nest budding, or active division of a *Nasutitermes* colony, involves construction of a satellite nest that remains, for at least some duration, connected to the healthy original nest by galleries and termite traffic between the two (or more) nests (Thorne 1982a, 1984; Levings and Adams 1984; Atkinson and Adams 1997; for further discussion of budding in termites, which can also be a passive process, see Nutting 1969, Thorne et al. 1999). Nest relocation occurs when a colony abandons its original nest and

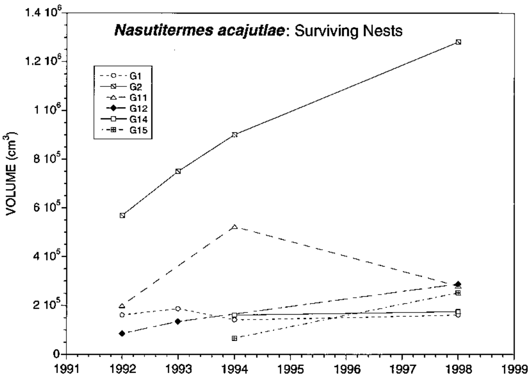

Fig. 8. Growth of *N. acajutlae* nests on Guana Island that survived until October 1998. Growth of relocated nests is not shown.

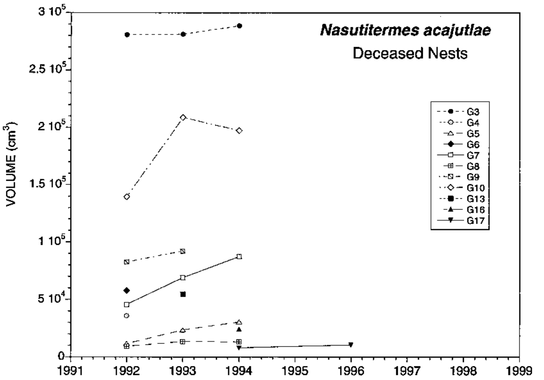

Fig. 9. Growth of *N. acajutlae* nests on Guana Island that died before October 1998.

moves in entirety (including the physogastric queen) into a freshly constructed nest. From our observations, the circumstances initiating such a move always involved dislocation and often substantial injury to the original nest following a fall from its host tree or being tipped over in a mass of fallen branches during a storm. The new nest sites that we observed were all within 10 m of the downed nest, often closer. In one case on Guana Island, an *N. acajutlae* colony (G11) had previously constructed a small, satellite unit of thin carton, apparently used as a foraging hub without reproductives or brood. When the main nest was knocked down, apparently by a storm, the colony relocated into the already established satellite nest, which was rapidly expanded.

Resprouting of a colony occurs when a nest is totally destroyed or removed (as by an armadillo, anteater, or human), and the orphaned termites that remain in the colony's gallery network and foraging locations consolidate and build a new nest. If it is an opportune time of year with alates mature or in development, then alates within the nest may develop into adultoid reproductives and carry on growth of the colony. If nymphs or alates are not present, worker *Nasutitermes* may differentiate into functional ergatoid reproductives under some circumstances (Thorne and Noirot 1982, Noirot and Thorne 1988), or the resprouted nest may remain without reproductives and survive only until its cohort of workers senesce.

B.L.T. observed all three of these rapid nest creation processes in Panamanian *N. corniger*, and documented nest relocation and resprouting in *N. ephratae* in the same habitat. Both authors witnessed relocation of two of the *N. acajutlae* nests in our Guana Island study area, and previously B.L.T. and Margaret Collins observed relocation of a third nest and resprouting of another, also on Guana Island.

Incipient Nests. Long-term observation and familiarity with the sites enabled us to recognize and study newly appearing nests in both the Panama and Guana Island research plots. In Panama, during the course of 2 yr early in the rainy season, B.L.T. observed the appearance, virtually overnight, of four *N. corniger* nests, each 7–10 cm in diameter (nearly spherical, therefore ≈180–524 cm^3) and containing ≈10,000–16,000 termites (nest only; excludes individuals in foraging galleries and at food sources) (Thorne 1984). On three occasions she found small incipient colonies housed completely within wood, one of which she collected and dissected. That decaying log had no termite carton inside except around a knothole, which was later found to house the tiny royal cell, less than 1 by 1 cm. The primary king and queen inside weighed 0.0063 and 0.0152 g, respectively (wet weights). Approximately 2,000 termites accompanied the royal pair in a 20-cm section of the log.

Arboreal *N. corniger* and *N. ephratae* nests frequently surround a trunk or branch which, when exposed after nest dissection, often contains a hollowed cavity or knothole that served as the original royal cell. In small nests the royal pair may still be lodged in wood; in larger nests the royal cell is generally constructed adjacent to the original copularium. We suggest that the probable ontogeny of arboreal *N. corniger* colonies is that the royal pair remains sequestered in their original copularium embedded in wood for several years as their incipient colony grows. Workers and soldiers in the young colony also remain within the wood, first eating local areas of the host tree and eventually traveling through the tree core, or perhaps building external galleries, to other food sources. Colonies also may be initiated in stumps or logs. When the colony population size approaches 10,000 termites, and when the first rains of the wet season create the right conditions, the colony blossoms into a rapidly constructed arboreal nest, normally adjacent to the royal cell, roughly 10–12 cm in diameter. In this proposed sequence of colony development, arboreal termites remain hidden within their host wood until their colony population size reaches a point that they can repair, maintain, defend, and ultimately expand a visible and exposed nest, although a freshly constructed, small nest remains quite vulnerable. Although some incipient colonies were found within logs, all observed new nests were on trees. This suggests that founding

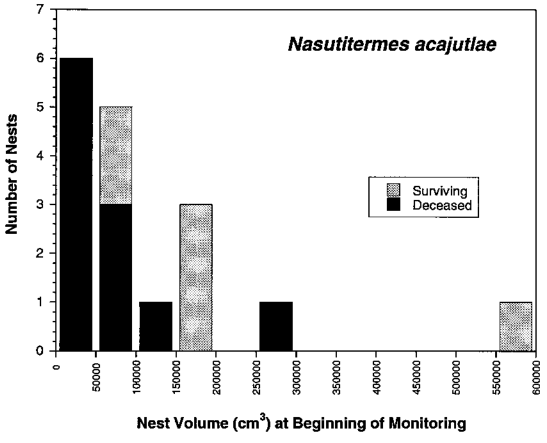

Fig. 10. Survivorship of *N. acajutlae* nests based on size at the beginning of monitoring.

pairs within trees have a higher probability of survival, or that colonies that begin in wood on the ground may move to a tree before or during nest construction. The size of a colony, and its queen, at the time of first nest construction may influence its subsequent rate of growth.

Nasutitermes acajutlae nests on Guana Island were monitored only at yearly intervals so it is impossible to precisely age new recruits or to know their size when they first appeared as carton nests. However, in 1998 we found three new nests that had not been present in 1997. Those nests had volumes of 17,981, 7,950, and 7,037 cm^3. We have never seen a *N. acajutlae* nest smaller than 7,000 cm^3 in any habitat, so if they remain cryptic within wood and then "bloom" as does *N. corniger*, a size of $\approx$7,000 cm^3 may reflect their usual debut size as arboreal nests.

Discussion

There have been very few studies of long-term nest growth and/or survivorship in termites. Banerjee (1975) monitored growth of five incipient colonies of *Odontotermes redemanni* (Wasmann) in India for 2 yr, finding that the annual growth rate of individual mounds was higher for smaller mounds ($<$75 cm in height) than for larger mounds ($>$100 cm in height). All five of the mounds that he followed survived the 2-yr study. Roonwal (1977) studied the ratio of height to diameter expansion during growth of mounds of three species of *Odontotermes* in India, determining that the growth pattern was allometric. Korb and Linsenmair (1998) conducted the most detailed demographic study yet completed on termites, measuring a variety of fitness parameters (probability of survival, age of first reproduction, number of alates produced per colony, and lifelong probability of reproduction) on individual *Macrotermes bellicosus* (Smeathman) mounds in an Ivory Coast savanna. This work will be a landmark study when published.

The results of our work on three species of Neotropical, arboreal *Nasutitermes* suggest that a relatively low percentage of individual nests survive for the long term, at least in the sites that we studied. Smaller nests of *N. acajutlae* had lower survivorship than larger nests within this study; the probability of survival of small and large *N. corniger* nests was indistinguishable among nests in this study. Our sample of *N. ephratae* nests was too small to evaluate the association of size and probability of survival. Both the Panama and Guana Island sites were free from human perturbation, but had other risks for termites. In Panama there were anteaters that can climb trees and swipe their sharp claws into *Nasutitermes* nests (Lubin and Montgomery 1981). Once a nest is injured, there are many species of predaceous ants that readily invade *Nasutitermes* colonies. B.L.T. observed *Camponotus* sp. ants clean out an injured *N. corniger* nest in $<$24 h. Anteaters, ants, or armadillos may attack *Nasutitermes* nests cracked or otherwise damaged after falling from their host tree during a storm. In contrast with Panama, no vertebrate termite predators live in the British Virgin Islands other than lizards that eat termites exploring outside of their nest or galleries. During our 9-yr study, the largest cause of mortality to *N. acajutlae* nests on Guana Island appeared to be hurricanes, with drought stress as another possibly signficant factor. Hurricanes create termite food and habitat by downing trees and branches, but the storms may also dislodge and injure established nests, causing death or inducing the colony to relocate. Inter- and intraspecific competition and territorial interactions among neighboring *Nasutitermes* may also affect growth and survivorship of nests (Thorne 1982a; Levings and Adams 1984; Adams and Levings 1987; Leponce et al. 1995, 1996, 1997). In all three species, the survivorship information presented here does not include the earliest age classes of colonies, which begin sequestered within wood and are therefore invisible to scientists in this type of survey.

In this study we report on the growth and survivorship of individual nests, as opposed to colonies because some *Nasutitermes* are polydomous, meaning that a single intermingling colony may construct and occupy more than one nest (Levings and Adams 1984; Roisin and Pasteels 1986; Adams and Levings 1987; Clarke 1993; Leponce et al. 1995, 1996, 1997; Atkinson and Adams 1997; Thompson and Hebert 1998a, b). Although *N. corniger* colonies are known to form buds and occupy those satellite nests in some habitats (Thorne 1982b, 1984; Levings and Adams 1984; Adams and Levings 1987; Atkinson and Adams 1997), we feel confident that the *N. corniger* nests monitored in this study were each single colonies, not interconnected buds. None of the trails leading from *N. corniger* nests was connected to any other nest. Termites from all nests in the site were evaluated for agonistic behavior in pairwise bioassays, always resulting in aggressive interactions between neighboring nests (Thorne 1982a). The queenright condition of surviving nests, determined upon dissection, suggests that they were independent colonies. Furthermore, the habitat had been cleared of larger trees and burned 3–6 yr previously, so although the *N. corniger* colonies in our study may have been founded before the habitat destruction, they bloomed into arboreal nests within a relatively few years of the beginning of the study. They were thus generally too young to bud, although two of the colonies were observed in the process of budding during the study.

Nasutitermes ephratae colonies are not yet known to bud; the seven in this study were spatially dispersed and almost certainly represented individual colonies. Little is known of colony structure in *N. acajutlae.* Although the monitored nests on Guana appear to represent independent colonies because of a scattered spatial configuration, colonies of the closely related species *N. nigriceps* (Thorne et al. 1994, 1996b) may occasionally occupy more than one nest (Levings and Adams 1984, Clarke and Garraway 1994). Further study of *N. acajutlae* is needed before we can fully interpret the association between nests and colonies.

In both *N. corniger* and *N. ephratae,* nest expansion was confined to the wet season during our study, the only exception being growth of some budded nests. Termites need rain for moisture to open existing walls and effectively masticate materials needed to build additional galleries (Thorne 1984). Colonies may be forced to repair nests during the dry season if that is when an injury occurs, but volume expansion appears to be restricted to the wet season. The occasionally enormous growth rates observed during the course of the wet season may reflect accommodation of a population increase that already occurred, and/or anticipation of growing ranks in the near future. Seasonal patterns of nest growth, particularly following rains, was also noted by Noirot and Noirot-Timothée (1962) in *Cubitermes fungifaber* (Sjöstedt) and by Bodot (1967) in *Amitermes evuncifer* Silvestri, *Cubitermes severus* Silvestri, and *Trinervitermes trinervious* (Rambur) on savannas of the Ivory Coast. Banerjee (1975) reported an inverse relationship between mound building and rainfall in the Indian termite *Odontotermes redemanni* (Wasmann), with reduced construction during heavy rains.

The ability of termite colonies to relocate to a new nest site has been documented in several species. Emerson (1929) witnessed migration of a colony of *Nasutitermes costalis* (Holmgren) including the royal couple, and Emerson (1938) made a persuasive case that every visible arboreal *Constrictitermes cavifrons* (Holmgren) nest is the result of a colony migration because the nests are constructed on living trees with smooth bark, and there is no evidence of excavation of a royal cell into bark beneath the nests. Noirot and Noirot-Timothée (1962) describe nest relocation in *Cubitermes fungifaber* in the Ivory Coast. In the cases of nest relocation that we observed in *N. acajutlae, N. corniger,* and *N. ephratae,* colonies abandoned their original nest and moved to a newly built replacement following major disturbance, such as the nest falling to the ground or becoming angled at a severe tilt following storm damage or decay of the host tree. The original nest sometimes was not visibly injured, but repositioned, often in a more vulnerable site.

Growth rates and survivorship of termite nests of a particular species are almost certainly influenced by habitat, season, inter- and intraspecific competitors, and disturbance from predators, drought, storms, and humans. For example, all *N. corniger* nests monitored in this study were in an area of young second growth, a habitat characterized by high vegetative productivity, an age distribution skewed toward young colonies, rapid succession of the young forest and therefore of nest sites, and moderate predator pressure (Thorne 1984). Nest and colony growth and survival rates in this young habitat may be quite different than in a primary forest.

Species of arboreal *Nasutitermes* appear to be remarkably adaptable and resilient, capable of colony budding, relocating, and resprouting to expand and/or adjust to changing circumstances or destruction of the original nest. Despite this flexibility, long-term survivorship of arboreal *Nasutitermes* nests and their associated colonies is low, even though these conspicuous nests appear to be abundant in many Neotropical habitats. Conservation of social insects has only recently been established as an important issue; colonies are now recognized to be more vulnerable than they appear on the basis of numbers of individuals (Pamilo and Crozier 1997). Because of their ecological importance as decomposers, and because they have a lower survival rate than previously predicted, efforts should be made to preserve active *Nasutitermes* nests in natural communities.

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