Research article

Acanthocephalan (Oligacanthorhynchidae) parasitism of the Caribbean termite *Nasutitermes acajutlae*: implications for reproductive success

C.A. Fuller and P. D. Jeyasingh

1 Department of Biology, Murray State University, 334 Blackburn Hall, Murray, KY 42070, USA, e-mail: claire.fuller@murraystate.edu, puni@ou.edu

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Summary. Few studies have examined the impact of parasitism on free-living social insects. We documented the association between an acanthocephalan parasite and survival, reproduction and growth of a Caribbean termite (*Nasutitermes acajutlae*). We measured these parameters yearly in >100 termite colonies for 4 years. In 2001 and 2002 we also compared the rate at which parasitized and unparasitized colonies rebuilt damaged foraging trails because trails protect foragers from predation as well as fluctuations in temperature and humidity. Although there were no significant differences in growth or survival between parasitized and unparasitized colonies, parasitized colonies reproduced significantly less often and rebuilt foraging trails significantly more slowly than unparasitized colonies. The average parasitized colony may sustain a loss of alate production ≥30% in the year in which it is parasitized, and a loss of up to 19% if it is parasitized once in a 5-year period. We conclude that the acanthocephalan parasite is associated with significant alteration of fitness parameters of individual *N. acajutlae* colonies. However, prevalence of parasitism is low (6.8%) and alate production by non-parasitized colonies is likely to compensate for losses due to parasitism. Therefore, it seems unlikely that this parasite affects *N. acajutlae* at the population level.

Key words: *Nasutitermes*, Acanthocephala, parasite, reproduction, Caribbean.

Introduction

Termites are one of the most important degraders in tropical ecosystems (Wood and Sands, 1978). As a whole, they are thought to be responsible for as much as 20% of carbon mineralization (Bignell and Eggleton, 2000), and can therefore be considered ecosystem engineers (Sugimoto et al., 2000). Numerous studies document the composition of termite communities, their role in ecosystems (reviewed in Bignell and Eggleton, 2000) and the factors that affect their population dynamics (Lepage and Darlington, 2000). *Macrotermes bellicosus*, a fungus-growing tropical termite, has received the most attention to date. Factors influencing *M. bellicosus* include predation (Lepage, 1984; Korb and Linsemann, 2002), competition (Korb and Linsemann, 2001) and temperature (Korb and Linsemann, 1998). Studies in other species have also found that food resources, predation and abiotic factors such as moisture often play an important role (reviewed by Lepage and Darlington, 2000).

In contrast, the effect of parasites on termite population parameters has received little attention. Parasites of termites may have an especially large impact on ecosystem processes because both the host and the parasite may function as ecosystem engineers (Thomas et al., 1999). A number of studies document the presence of fungal, arthropod and nematode parasites in naturally-occurring termites (reviewed in Schmid-Hempel, 1998). Some studies also document the effects on individual termites or laboratory-reared colonies (Schmid-Hempel, 1998). However, studies documenting the impact of parasites concentrate on a few species of termites and most have examined laboratory populations.

We studied the effect of an acanthocephalan parasite (Family Oligacanthorhynchidae; B. B. Nickol, pers. communication) on the life history of the higher termite, *Nasutitermes acajutlae* (Holmgren). The life cycles of all acanthocephalans are similar: adults live in the intestine of the vertebrate definitive host and shed eggs with the hosts’ feces. The arthropod intermediate host becomes infected by eating parasite eggs. Transmission from the intermediate host to the definitive host occurs via predation (Roberts and Janovy, 2000). We do not yet know the definitive host of the termite acanthocephalan, although we believe it is a bird because most oligacanthorhynchids use birds.

As in many eusocial organisms, *N. acajutlae* has distinct morphological castes. In this genus, the castes consist of workers, soldiers and reproductives (Roisin and Pasteels,
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 defense compound. Reproductive in a colony consist of at least one king and queen that produce the other castes. Female *N. acuajutlae* workers show the highest incidence of acanthocephalan parasitism within colonies (>99% of infected termites are female workers) and up to 70% of foraging workers can be infected (Fuller et al., 2003). The termite acanthocephalan is associated with behavioral and morphological changes in infected termites that increase exposure to predation (Fuller et al., 2003). Because female workers are the most numerous animals in *Nasutitermes* colonies, typically making up >60% of the colony biomass (Thorne, 1985; CAF unpubl. data), and perform the majority of foraging and maintenance activities, a parasite that has a large effect on them has the potential to have a strong impact on the colony as a whole.

We conducted a long-term (4 yr) observational study of >100 *N. acuajutlae* colonies on the island of St. John, US Virgin Islands. Specifically, we tested the hypothesis that the acanthocephalan parasite alters key life-history traits of *N. acuajutlae*. We tested the predictions that parasitism is associated with reduced longevity, reproduction, and growth rates. We also conducted a trail rebuilding assay because the arboreal nest of *N. acuajutlae* and their covered foraging trails are thought to be important in reducing predation and regulating nest temperature and humidity (Jones, 1980). Thus we predicted that parasitized colonies rebuild more slowly than unparasitized colonies.

**Methods**

**Study sites:**

St. John, USVI is small (492 km²) and steep with max. elevation of 370 m. It is considered to be a tropical dry island, with rainfall below 130 cm per year and temperatures ranging between 21 to 35°C. St. John is sparsely populated (<4000 people) and 2/3 of the island is a national park (Virgin Islands National Park). *Nasutitermes acuajutlae* occurs in all areas of the island, building large arboreal nests and covered foraging trails out of fecal material and saliva. It is the only member of this genus known to occur on St. John (Jones and Nalepa, 2002).

**Long-term observations**

We began this study in June/July of 1998. We chose sites in accessible locations throughout St. John and marked as many colonies in these areas as we could find. Each colony was marked with a metal tree tag for future identification. We determined whether colonies were parasitized by opening a stretch of trail (generally ~15 cm) and watching for parasitized termites. Fuller et al. (2003) demonstrated that parasitized workers generally come to trail breaks in <10 s (X = 5.8 ± 4.9 SE). If no parasitized termites appeared in the opening within 5 min, we considered the colony to be unparasitized. It is likely that we missed some parasitized colonies using this procedure. However, observations in which we repeatedly assessed the same colony for >10 min indicated that missed colonies have very low parasitism (only 1% of workers parasitized), thus are unlikely to be significantly affected by parasitism. We estimated the percent of foraging workers that were parasitized during each field season by scraping 15–30 cm of trail sample into a container along with the termites that were in the trail. We scraped these trails rapidly, from either end of the break inward to insure we only collected termites that were foraging in the scraped trail. We identified parasitized workers by their color and by dissection. We determined survival and the presence of secondary reproductives by taking at least one core sample with a soil corer (1.9 cm diameter). If cores contained active termites, we considered the colony to be alive; if they contained nymphs in any instar or alates, we considered the colony to be reproductively active. We estimated colony biomass using the methods of Levington and Adams (1984); 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 (4/3π*r1*r2*r3). During subsequent visits (June/July of 2000, 2001 and 2002), we re-measured and re-examined colonies for parasites and alates. 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), we divided growth by 2. Finally, we marked new nests that we encountered as we expanded the size of our monitored area. Most marked colonies were assessed for survival and parasitism each year except for a few colonies we were unable to find in 2000. However, 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 examine the relationship between parasitism and survival. Table 1 shows the number of new and revisited colonies examined each year.

**Rate of trail rebuilding**

We performed pair-wise comparisons between parasitized and unparasitized colonies. Paired colonies were approximately equal in volume to control for differences in number of workers (Levington and Adams, 1984). In addition, paired comparisons were made during the same time of day to eliminate temperature-dependent responses to trail rebuilding rates. Each colony was only used once. One cm² of the main foraging trail was broken approximately one meter below the nest. Immediately thereafter, the break was marked with a tag that had a 1 cm scale on it, and a photograph was taken. The break was revisited after exactly 30 min and another photograph was taken. The pictures were digitized and the amount of gallery rebuilt was measured using Scion Image® software.

<table>
<thead>
<tr>
<th>Year</th>
<th>Newly marked</th>
<th>Biomass measured</th>
<th>Sampled for alates</th>
<th>Alive next period</th>
<th>Biomass measured next period</th>
<th>Sampled for alates next period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>102</td>
<td>79</td>
<td>74</td>
<td>71</td>
<td>46</td>
<td>39</td>
</tr>
<tr>
<td>2000</td>
<td>24</td>
<td>15</td>
<td>6</td>
<td>80</td>
<td>59</td>
<td>59</td>
</tr>
<tr>
<td>2001</td>
<td>19</td>
<td>17</td>
<td>15</td>
<td>85</td>
<td>64</td>
<td>63</td>
</tr>
<tr>
<td>2002</td>
<td>28</td>
<td>26</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1. The number of new nests marked each year and the number from previous years. Sample size can be obtained from this frame for any category or any year. E.g., total marked nests in 2002 was 28 + 85 + 113. Total number of nests sampled for alates in 2001 was 15 + 59 = 74.
Statistics

We examined the relationship between parasitism and survival and parasitism and alate production using logistic regression models. We used log-transformed nest volume as a covariate in these models because colonies may be more likely to survive and produce alates as they increase in size (Thorne and Haverty, 2000). We used a backwards stepwise procedure to exclude any variables from models that had alpha levels >0.10. We used an ANCOVA to examine colony growth, with initial nest volume as a covariate, because initial nest volume could affect growth rate if larger colonies have more workers to add to the nest. Both the covariate and growth (year 2 volume – year 1 volume) were log-transformed.

We included colonies in the logistic regression and ANCOVA models each time they were sampled (Table 1) because of limited sample size of parasitized colonies. This procedure assumed that each sample was independent of other samples for a given colony. We tested these assumptions as follows: first, for alate production, we examined whether alate production in one year (year 2) was affected by whether the colony had produced alates the previous year (year 1). We used samples from 2 periods (2000–2001 and 2001–2002); we excluded parasitized colonies and only included each unparasitized colony once. We included sampling year, nest volume in year 1 and nest volume in year 2 as effects/covariates in the logistic regression model. We used a backwards stepwise procedure to eliminate non-significant (P > 0.10) variables. In the final model only volume in year 2 explained a significant portion of variation in alate production in year 2 (F_{par} = 12.6, df = 1, 55, P = 0.001); alate production in year 1 did not (F_{nest} = 2.61, df = 1, 55, P > 0.1). Second, to test the assumption that growth in one year is unaffected by growth in the previous year, we correlated growth from 2000–2001 with growth from 2001–2002 for all colonies that were measured in each of these years. We did not find a significant relationship (r = -0.01, N = 38, NS), suggesting that growth in one year does not affect growth the following year.

The percent of trail rebuilt in 30 min was arcsine transformed and compared between parasitized and unparasitized colonies using a paired t-test.

Results

Prevalence of parasitism among and within colonies

Overall, the prevalence of parasitism among colonies was 6.8% (Table 2). Of the 25 colonies that were parasitized during the study, 22 were parasitized in year 1 and 3 were parasitized in 2 years. Of these, 1 was parasitized in 1998 and 2000; the other 2 were parasitized in 1998 and 2001. The mean percent of foraging workers that were parasitized in parasitized colonies was 22.03 (± 5.18 SE) (Table 2). Parasitized colonies were not found in the smallest (<45 L) and largest (>450 L) size classes (Fig. 1) but did not differ significantly in size from unparasitized colonies (45–450 L size class only; ANOVA; F_{par} = 0.14, df = 1, 247, P = 0.71). In further analyses, we only included colonies in the 45–450 L range.

Figure 1. Size distribution of 25 parasitized (open bars) and 284 unparasitized colonies (gray bars). Parasitized and unparasitized colonies did not differ significantly with respect to size distribution, however, parasitized colonies did not occur in the smallest and largest size classes.

Table 2. Number of colonies parasitized and prevalence of parasitism among foraging workers in each year of the study. Numbers in parentheses are SE and the number of parasitized nests sampled

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of colonies parasitized</th>
<th>Percent of foraging workers parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>16 of 102 (16; 91, 10)</td>
<td>36.6 (9.1, 10)</td>
</tr>
<tr>
<td>2000</td>
<td>1 of 95 (1; 1)</td>
<td>25 (--; 1)</td>
</tr>
<tr>
<td>2001</td>
<td>6 of 99 (6; 2, 1)</td>
<td>4.9 (2.1, 6)</td>
</tr>
<tr>
<td>2002</td>
<td>5 of 113 (5; 2, 5)</td>
<td>12.7 (5.2, 5)</td>
</tr>
</tbody>
</table>

Colony survival

Table 3 shows the survival of parasitized and unparasitized colonies for each interval of the study. We were unable to include year as a factor in the model examining the relationship between parasitism and survival due to small sample sizes of parasitized colonies in some years. However, there was no significant relationship between year and survival of unparasitized colonies (F_{year} = 0.1, df = 2, 180, P = 0.89; F_{nest} = 23.5, df = 1, 180, P < 0.001). Therefore, survival data were pooled across years. The interaction between nest volume and parasitism was not significant (F = 0.9, df = 1, 180, P = 0.33) and was excluded from the logistic regression model. Although nest volume was significantly related to colony survival (F_{nest} = 24.44, df = 1, 181, P < 0.001), parasitism was not (F_{par} = 0.3, df = 1, 181, P = 0.58).

Table 3. Survival of parasitized and unparasitized colonies for each sampling interval. Data include only colonies that are in the same size classes as parasitized colonies (45–450 L).

<table>
<thead>
<tr>
<th>Status</th>
<th>1998–00</th>
<th>2000–01</th>
<th>2001–02</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parasitized</td>
<td>13/15</td>
<td>0/1</td>
<td>5/5</td>
<td>18/21</td>
</tr>
<tr>
<td>(86.7)</td>
<td>(0)</td>
<td>(100)</td>
<td>(85.7%)</td>
<td></td>
</tr>
<tr>
<td>Unparasitized</td>
<td>39/54</td>
<td>44/52</td>
<td>56/68</td>
<td>139/174</td>
</tr>
<tr>
<td>(72.2)</td>
<td>(84.6)</td>
<td>(82.3)</td>
<td>(79.9)</td>
<td></td>
</tr>
</tbody>
</table>
Colony reproduction (alate production)

Alate production did not differ by year either for all colonies (Logistic regression, $F_{\text{nest}} = 0.417, df = 3, 251, P = 0.74$) or when parasitized colonies were excluded ($F_{\text{nest}} = 0.90, df = 3, 224, P = 0.44$). Therefore, the data were pooled across years in further analyses. The parasitism*nest volume interaction was not significant (Logistic regression, $F = 0.005, df = 1, 234, P = 0.88$). When the interaction term was excluded from the analysis, both colony size ($F = 4.75, df = 1, 235, P < 0.001$) and parasitism ($F = 4.75, df = 1, 235, P = 0.03$) were significantly related to the occurrence of alate production (Fig. 2). It is possible that parasitized colonies are intrinsically less likely to produce alates than unparasitized colonies that were never parasitized. Therefore, we determined whether parasitized colonies were also less likely to produce alates than unparasitized colonies during years in which parasitized colonies were not parasitized. Again, the parasitism*nest volume interaction was not significant ($F = 0.17, df = 1, 212, P > 0.50$) (Note that, in this case, parasitism indicates colonies that had been infected during the study but were not infected when included in this analysis). When the interaction term was excluded from the analysis, only nest volume had a significant effect on alate production ($F_{\text{nest}} = 33.8, df = 1, 213, P < 0.001; F_{\text{par}} = 1.7, df = 1, 213, P = 0.19$).

Growth of parasitized colonies

There was no effect of year on size classes of parasitized and unparasitized colonies (45–450 L size class only; ANOVA; $F_{\text{par}} = 0.8, df = 3, 247, P = 0.49, F_{\text{year}} = 0.16, df = 3, 247, P = 0.92$). We were unable to include year as a factor in the model examining the relationship between parasitism and growth rates due to small sample sizes of parasitized colonies in some years. However, when the relationship between year and growth was examined independently of parasitism, colony growth did not vary with year ($F_{\text{year}} = 0.861, df = 2, 149, P = 0.425$). Therefore, we examined the relationship between parasitism and nest volume for all years pooled. Nest volume was significantly related to growth ($F = 12.344, df = 1, 150, P = 0.001$) but parasitism was not ($F = 1.57, df = 1, 150, P > 0.20$).

Rate of trail repair

Parasitized colonies repaired a 1 cm² break in their trails significantly more slowly than unparasitized colonies (paired $t = 2.37, P < 0.05, N = 13$; Fig. 3).

Discussion

Our study showed that parasitized colonies did not produce alates as frequently as similar-sized unparasitized colonies. Moreover, parasitized colonies rebuilt broken foraging trails significantly more slowly than unparasitized colonies. However, there was no evidence that parasitism negatively affected colony survival or growth. Because this study is observational, it is not possible to determine whether the parasite caused the differences in alate production and trail rebuilding. However, colonies had normal alate production in years during which they were unparasitized, suggesting that parasitized colonies did not have inherently low alate production. In addition, we found significant differences in trail rebuilding rates when colonies were paired to minimize differences in other factors (size of worker force and microclimate) that might have affected rebuilding rates.

The effect of a decrease in reproduction in one year may have a large impact on long-term fitness, especially for...
smaller parasitized colonies because these colonies grow more slowly and have poorer survival than larger colonies. For example, 66% of parasitized colonies are in the 100–200 L size class (Fig. 1). On average, they are 33.6% less likely to produce alates in the year of parasitism. Most colonies will not reach the next size class by the end of a 5-yr period because growth is slow (17.4 ± 5.4 L in this size class, our data) and only 43.5% will still be alive (the probability of survival for this size class = 0.812 per year, our data). Thus, the average loss in terms of the frequency of alate production is 19% over 5 years, if a colony is parasitized once in this period. We did not measure the number of alates produced. However, it seems likely that parasitized colonies also produced fewer alates for a given colony size than unparasitized colonies, exacerbating the fitness loss still further. Although it is possible that colonies undergo some compensatory alate production after parasitism, it seems equally likely that alate production is negatively impacted after parasitism.

The mechanisms that decrease alate production and rebuilding rate are unclear. Parasitized workers spent more time in exposed locations of broken trails than unparasitized workers (Fuller et al., 2003) and, presumably, less time rebuilding trails. Thus parasites may reduce the number of workers that rebuild broken trails. There are at least 3 possible ramifications of decreased rebuilding: first, nests and trails help maintain colony temperature and humidity (Jones, 1980, describing *N. costalis*), therefore, breaks in trails should compromise the colonies’ microclimate. Second, Fuller et al. (2003) demonstrated that parasitism is associated with an increase in vulnerability to predation; parasitized workers undergo a color change that increases the likelihood that they are eaten by lizard predators, compared to their unparasitized counterparts. Presumably, parasitized workers continue to have increased exposure and predation risk until trails are patched. Thus, the decreased rate of trail rebuilding should further increase exposure to predation of both parasitized and unparasitized termites. Korb and Linzenmair (2002) found that *Macrotermes bellicosus* abandoned patches of food significantly faster under increased predation pressure, thus increased predation on parasitized colonies could decrease foraging overall. Finally, workers bring food back to the nest for the dependent castes (reproductive, soldiers and immatures); any factor that significantly impacts their numbers or foraging behaviors could stress the colony energetically. This could induce the colony to stop alate production. However, we have not directly measured the difference in predation rates between parasitized and unparasitized colonies, or how microclimate might affect alate production. Moreover, it is difficult to quantify the amount of food brought into the colony by workers to directly compare net foraging rates of parasitized and unparasitized colonies. Thus it is unclear whether these factors alone can explain the decrease in reproduction.

Other studies have documented the presence of numerous pathogens and parasites in naturally-occurring termites (Schmid-Hempel, 1998). A few, including bacteria (e.g., Connick et al., 2001), fungi (e.g., Jones et al., 1996; Rosen-
References


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