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Nest site selection and differential defense responses based on nest substrate in Neotropical termites (Nasutitermes spp.)

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Neotropical termites (*Nasutitermes* spp.)

by

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ABSTRACT

Nest site selection in a variety of species can be impacted by the assessment of predation risk. Predation risk can be evaluated by factors such as nest height, concealment, and substrate type. With the assumption that predation risk varies among substrate types, *Nasutitermes* spp. termites were predicted to non-randomly select nest sites based on substrate type and to display differential defense response as a function of substrate. If given vibratory cues prior to nest breach, *Nasutitermes* spp. termites were predicted to react to the breach more quickly or with more soldiers. Seventy five nests were surveyed at the Palo Verde Biological Station to record nest substrate type, nest area, nest coverage by vegetation, and potential nest sites within a 10m radius. Upon nest breach, the time to the first soldier's arrival and the subsequent number of soldiers that flocked to the disturbance site were recorded for each active nest. *Nasutitermes* spp. nest site selection reflected the availability of accessible substrate types rather than reflecting a preference for one type. There was no change in defense response in relation to substrate type or the presence of advance vibratory cues. *Nasutitermes* spp. nest site selection is not influenced by substrate type, suggesting that substrate types may not experience differential predation risk.

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INTRODUCTION

Predation pressures can have significant, direct impacts on prey morphology and behavior (Semlitsch 1987). Avoidance behavior may be active, such as the movement of marine gastropods out of the water or toward shelter (Cotton et al. 2004), or passive. Passive predator avoidance behavior can include an intentional change in microhabitat that alters prey species distribution (Main 1987, Semlitsch 1987). For example, caridean shrimp swim between grass blades to avoid the predatory pinfish (Main 1987) while the freshwater snail *Physella virgata* avoids crayfish encounters by crawling above the waterline (Alexander and Covich 1991). Nest site selection can act as a passive avoidance behavior that is simultaneously microclimatic and based on external factors surrounding the nest area (Martin and Roper 1988).

According to the threat-sensitive predator avoidance hypothesis, prey species are able to assess predation risk and adjust their defense response accordingly to minimize energy expenditure (Monclús et al. 2008). Nest placement is shown to significantly contribute to nest vulnerability (Li and Martin 1991), and predation risk may initially be assessed in nest site selection through various means. Nest predation risk may increase with proximity to the ground (Cresswell 1996; Li and Martin 1991), low nest concealment (Cresswell 1996), and low density of other potential nest sites surrounding the nest (Martin and Roper 1988, Martin 1993). Nest substrate choice may also significantly affect and be influenced by predation risk. For example, ruffed grouse females display a tendency to nest on stumps, logs, or at the base of large trees to decrease exposure to predators (Tirpak et al. 2006). Defense behaviors may change in

reaction to differential predation risk of a nest site. Common blackbirds (*Turdus merula*), while experiencing differential nest predation rates positively correlated with nest detectability, display differing nest defense strength among nest substrate types (Cresswell 1997). While good nest defenders can nest in a variety of substrates, poor nest defenders may be limited to concealed nest sites (Cresswell 1997).

Conspicuousness to predators may also differ among nest substrate types. Ruffed grouse females may choose to nest at the base of large trees, in stumps, and in logs because decreased ground cover enables predator detection (Tirpak et al. 2006). Several organisms are able to detect approaching predators via vibratory cues. For instance, the sand cricket has filiform hairs that are most sensitive to frequencies produced by approaching predators (Magal et al. 2006), while red-eyed tree frog embryos induce hatching based on vibration patterns associated with oncoming predators (Warkentin 2005). Drywood termites (*Cryptotermes domesticus*) use vibration signals to determine wood size and are able to discriminate the source of the vibrations (Evans et al. 2005). One focus of this study is to examine the potential for *Nasutitermes* spp. termites to detect predators by vibration cues as a function of nest substrate type.

In Palo Verde, *Nasutitermes* spp. termites have been observed to build nests on three substrates: lianas, shrubs, and trees (pers. obs.). While nests on lianas appear conspicuous, lianas have been noted to support and conceal the nests of various animals. The stingless bee, *Trigona opaca,* is shown to construct exposed nests around lianas (Roubik 1983), while the great antpitta, *Grallaria excels,* utilizes clumps of lianas to anchor nests to a vertical fork or tree trunk (Kofoed and Auer 2004).

This study tests the possibility of nonrandom nest site selection in *Nasutitermes* spp. termites nesting in lianas, shrubs and trees. If liana nests experience higher predation pressure due to greater conspicuousness or ease of access, then *Nasutitermes* spp. termites nesting in lianas may compensate for the increased predation risk by increasing the number of guarding soldiers or decreasing response time. In addition, if termites nesting in lianas are better able to detect vibrations made by an invading predator, they may increase the number of soldiers or decrease response time when presented a vibratory cue prior to nest breach as compared to nest breaches without the advance cue.

METHODS

This study was conducted in Palo Verde National Park at the Organization for Tropical Studies Biological Station in the Guanacaste province of Costa Rica (10° 21' N, 85° 21' W). The park comprises 19,000 ha of seasonally dry lowland tropical forest (sensu Holdridge 1947) and a RAMSAR-protected wetland within the Tempisque River Basin. The successional dry forest around the OTS Palo Verde Biological Station mostly comprises deciduous woody vegetation. The study was primarily conducted on the Pizote and Mapache trails as well as along the road extending East and West from the OTS Palo Verde Biological Station. Data for this study was collected from 25 February to 1 March 2013 between the hours of 0730 to 1200 and 1300 to 1800 CST.

The genus *Nasutitermes* is composed of tropicopolitan, advanced termite species with specialized castes and complex nests (Clarke and Garraway 1994). The two

Nasitutermes species located in Palo Verde are *N. corniger* and *N. costalis.* Most *Nasutitermes* species use wooden and carton materials during nest construction (Lubin and Montgomery 1981, Emerson 1938). These termites are unique in their lack of dependence on dirt and are therefore not confined by ground proximity during nest construction (Emerson 1938). Alates are responsible for initiating new colonization events; after nuptial flight their wings are shed and alate pairs begin to construct a nest on suitable substrate (Ferreira and Scheffrahn 2011). These termites can construct arboreal nests several meters above the ground and display plasticity in their site choice (pers. obs.). A major predatory threat to these termites in Palo Verde is the *Tamandua* anteater, which utilizes *Nasutitermes* spp. as a main food source (Lubin and Montgomery 1981).

Nasutitermes spp. soldiers have been observed to respond quickly to nest disturbances, including the breaching of the nest by poking a hole (Lubin and Montgomery 1981, Eisner et al. 1976, Stuart 1981), a method used for testing nest viability (Clarke and Garraway 1994). This method mimics the action of *Tamandua* attacks, whereby the anteater creates holes in termite nests with its foreclaws to consume the residing termites (Lubin and Montgomery 1981).

To determine whether *Nasutitermes* spp. discriminated among substrates when selecting nest sites, several *Nasutitermes* spp. nests within reaching level (generally at a height less than 2.2 m) were sampled. Each nest substrate type was scored as liana, shrub, or tree. The dbh (diameter at breast height) of the substrate was measured to the nearest tenth of a centimeter using a dbh tape. Length and width of the nest were measured to the nearest hundredth of a meter using a meter tape and later converted to

centimeters and multiplied to calculate nest area (cm^2). Percent nest cover by vegetation was used to quantify nest concealment. Nest cover was measured by walking 5 m North, South, East, and West of the nest and estimating the percentage of the nest area covered by foliage. The average of these four percentage values were calculated to obtain the percent nest cover value. The number of potential nest sites within a 10 m radius of the nest (number of lianas, number of trees, and number of shrubs) was also counted. Trees were distinguished from shrubs as having a height greater than 5 m. A potential nest site was considered to be a substrate with a dbh greater than 1 cm that was not already host to a termite nest.

To measure colony defense responses, a hole with a 2.5 cm diameter was made in each nest by poking a small stick into an area near the middle of the nest. Time to the arrival of the first soldier was recorded to the nearest second using a stopwatch. As *Tamandua* feeding bouts generally last less than three minutes and nasute soldier termites tend to defend the disturbance site for at least two minutes after an attack (Lubin and Montgomery 1981), the nest was observed for three minutes after the first soldier arrived at the disturbance site. The number of soldiers at the site of damage was recorded at each thirty-second period after the nest breach.

To test if *Nasutitermes* spp. alter their defense responses given vibratory cues, a separate trial was conducted using the same procedure as above with one change. One minute before nest breach, an area 0.5 m below the nest base was tapped twenty times to indicate predator approach. Trials with and without given advance cue were conducted

23.5-25.5 hours apart to provide time for colony recovery and resuming of normal activity while controlling for the time of day.

JMP Pro 10 (SAS 2012) was used in all statistical analyses. To determine whether nest size or nest coverage differed among nests on lianas, shrubs, or trees, two ANOVA tests were conducted. To test for non-random nest site selection, the number of potential tree, shrub, and liana nest sites was converted into percentage of potential nest sites for each focal nest and the percentages were summed to calculate the expected number of nests on each substrate. These expected values were compared to the observed number of liana, shrub, and tree nests using a Chi-squared Goodness-of-Fit test. To determine if defense response differed among substrates, time to the first soldier's arrival and number of soldiers 60 seconds after nest breach were compared among substrate types using two ANOVA tests. To determine whether the advance cue resulted in defensive response differences, two Student's T-tests were conducted between trials with and without prior cue of predator approach in regard to the two defense response variables: time to the first soldier's arrival and number of soldiers at 60 seconds.

RESULTS

A total of 75 nests were sampled: 25 tree nests, 27 shrub nests, and 23 liana nests. Only 21 nests displayed defense response behaviors, which comprised nine tree nests, seven shrub nests, and five liana nests. Six of these 21 nests failed to display defense response behavior in the trial with the advance cue. The remaining 54 nests appeared

abandoned, though eight displayed worker activity in the tunnels leading away from the nest.

All henceforth mentioned supplemental figures can be found in Appendix I. Mean nest cover and nest area did not differ among substrates (ANOVA, F = 0.3117, df = 2, p = 0.7332, R^2 = 0.0085, Figure 1; F = 1.4278, df = 2, p = 0.2466, R^2 = 0.0381, Figure 2). According to the Chi-Square Goodness of Fit test, *Nasutitermes* spp. displayed random nest site selection in relation to available substrate (df = 2, p = 0.05, χ^2 = 1.506). Additionally, neither defense response variable significantly differed among substrates with or without advance cue. The time to first soldier arrival and number of soldiers present 60 seconds after nest breach did not differ among substrates in trials without advance cue (ANOVA, F = 0.2542, df = 2, p = 0.7783, R^2 = 0.0275, Figure 3; F = 0.8057, df = 2, p = 0.4623, R^2 = 0.0822, Figure 4, respectively). Likewise, the time to first soldier arrival and number of soldiers present 60 seconds after nest breach did not differ among substrates in trials with advance cue (ANOVA, F = 1.1624, df = 2, p = 0.3432, R^2 = 0.1517, Figure 5; F = 1.7032, df = 2, p = 0.2203, R^2 = 0.2077, Figure 6, respectively). The time to the first soldier's arrival and number of soldiers 60 seconds after nest breach did not differ among nests in trials with and without advance cue (Student's T-test, t-Ratio = 1.3610, df = 14, p = 0.1950, Figure 7; t-Ratio = -1.5241, df = 14, p = 0.1498; Figure 8, respectively). Substrate type does not significantly influence nest site selection or defense response in *Nasutitermes* spp. termites.

DISCUSSION

Nest site selection is determined by a variety of abiotic, biotic, and ecological factors. A significant ecological factor to consider in nest site selection is the assessed risk of predation, which has been shown to differ among substrate types for some organisms (Tirpak et al. 2006).

Nasutitermes spp. exhibit random nest site selection in regard to substrate type and show similar defensive responses regardless of nest substrate. Non-preferential nest site selection based on substrate type suggests that predation risk does not significantly vary among nests in different substrates. Furthermore, *Nasutitermes* spp. in Palo Verde may experience similar or low levels of predation risk at the nest itself. Lubin and Montgomery (1981) proposed that *Tamandua* anteaters avoid termite nests and preferentially feed at logs and trails away from the nest. If so, *Tamandua* predation risk may play a minimal role in nest site selection.

Other biotic and abiotic factors should be considered in future studies concerning *Nasutitermes* spp. nest site selection. For instance, drywood termite alates are attracted to light and select nest sites that are the most highly lit (Ferreira and Scheffrahn 2011), a factor that was not accounted for in this study. Several microhabitat variables and aspects of the mosaic nature of the environment can be significant in determining species' distributions (Hutchinson 1959). Further studies focusing on nest site selection in *Nasutitermes* spp. could determine the significance of microhabitat and resource proximity factors.

While several organisms can make use of advance, vibratory information to avoid predators (Magal et al. 2006; Warkentin 2005), *Nasutitermes* spp. in Palo Verde do not appear to use vibrations along the nest substrate to induce a more rapid or greater defense. In addition, six of the 21 nests that defensively responded to nest breaches without advance cue did not respond to nest breaches when the advance cue was given. Soldiers in these nests may have retreated to the nest core upon sensing the vibratory cue; thus, the predator approach cue used in this study may have had its opposite intended effect. The method of tapping below the nest may not have effectively mimicked the vibrations generated by an approaching *Tamandua* anteater. I recommend that researchers pursue other methods to impersonate the advancing *Tamandua*.

I additionally suggest that researchers test the effects of other types of predation on *Nasutitermes* spp. defensive behaviors. In addition to anteaters and various birds, *Nasutitermes* spp. are consumed by a variety of ants and the assassin bug *Salyavata variegata* which covers itself in a camouflage made of *Nasutitermes* nest carton crumbs to aid in capturing termite prey at the nest (Pierce 1986). Predatory ants use a variety of strategies to collect termites, including facultative predation by individual foragers, organized attacks by worker ants, and predation by obligate termitophagous ant species (Traniello 1981). Extensive research has been done on the response of *Nasutitermes* spp. to nest breaches by mammalian and avian predators (Lubin and Montgomery 1981, Eisner et al. 1976, Stuart 1981, Clarke and Garraway 1994), though I recommend that more research be conducted on the responses of *Nasutitermes* termites to specialized

arthropod predation and to explore the potential for differential responses to these predation events due to nest site variables.

Nasutitermes spp. display random nest site selection in regard to nest substrate. Likewise, defense response does not differ among nests in different substrates and is not altered given prior vibratory cue of an approaching predator. The similarity of defense responses among tests with and without advance cues suggests that predation risk may not vary with nest location or that nests are defended at similar levels upon breaching, regardless of pre-predation vulnerability and vibratory cues.

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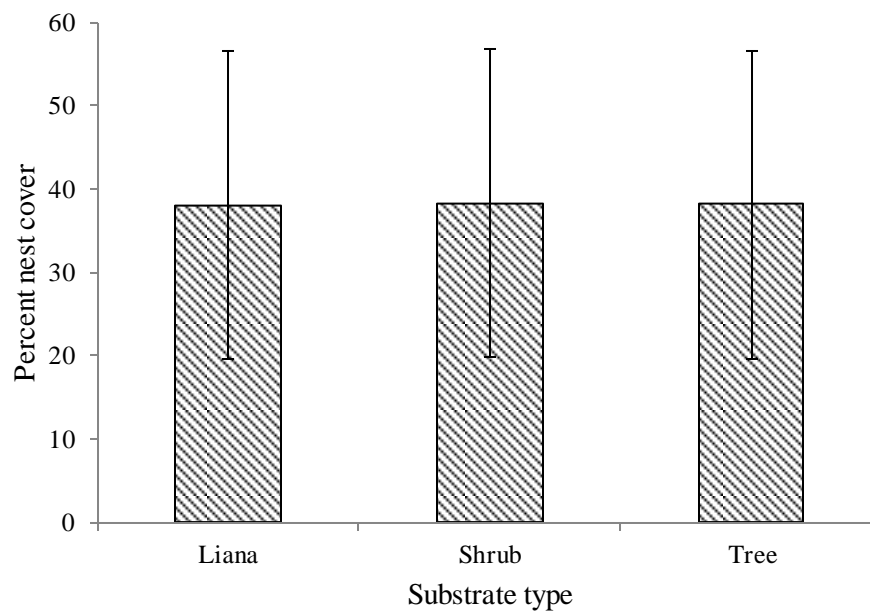
APPENDIX I

Figure 1: Nest cover of *Nasutitermes* spp. nests located in lianas, shrubs, and trees at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.
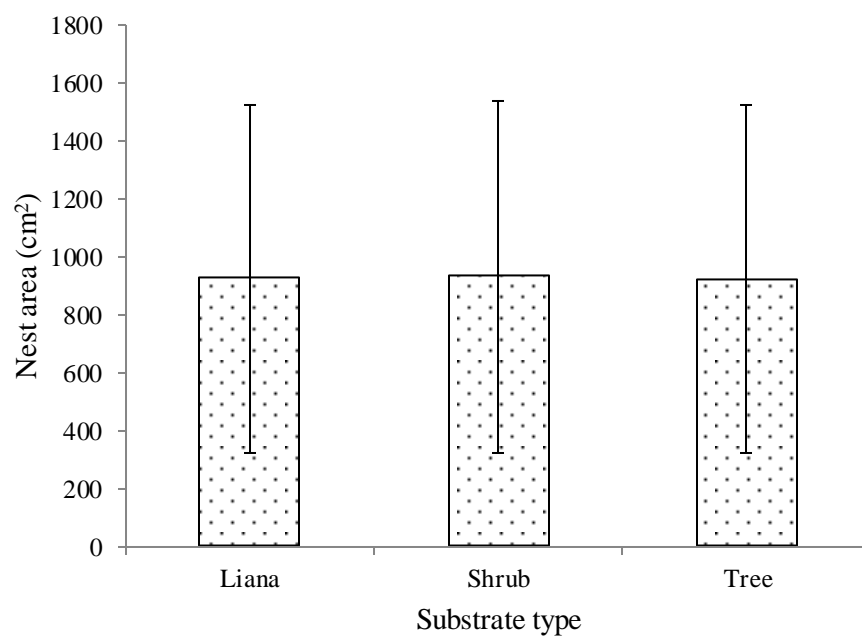

Figure 2: Nest area of *Nasutitermes* spp. nests located in lianas, shrubs, and trees at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.
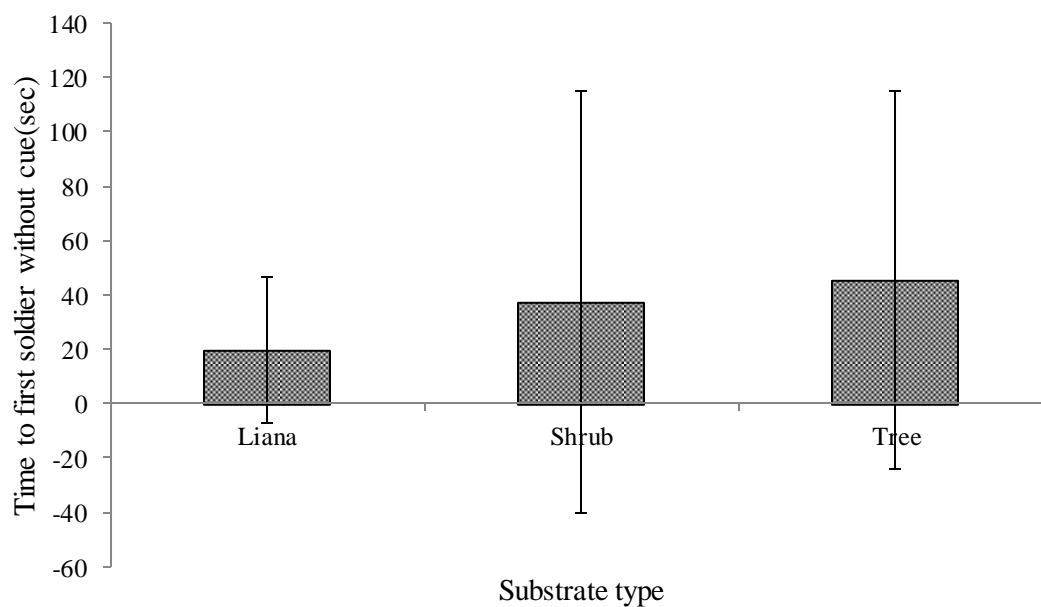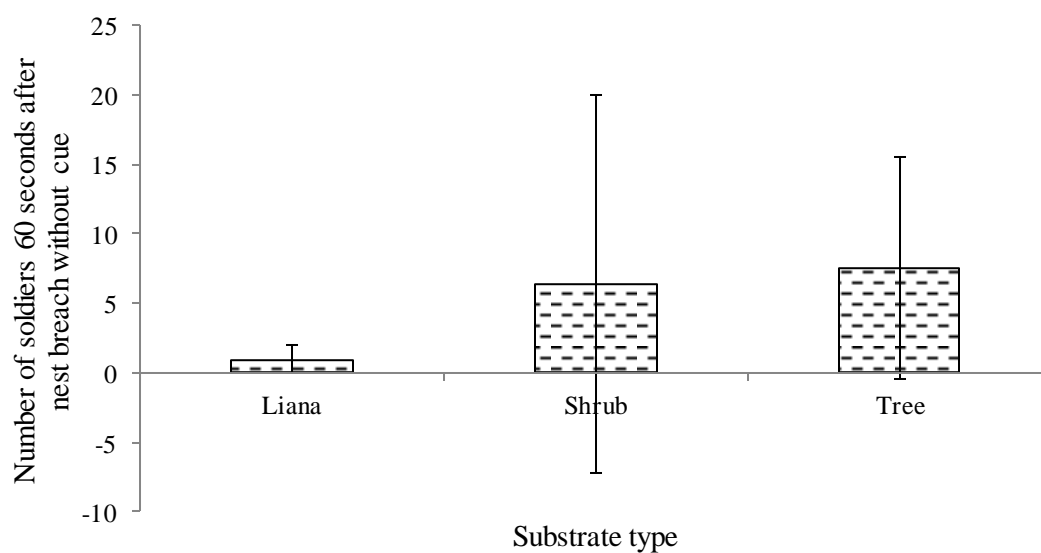
Figure 3: Time to first soldier arrival after nest breach for *Nasutitermes* spp. nests located in lianas, shrubs, and trees in trials without advance cue at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.
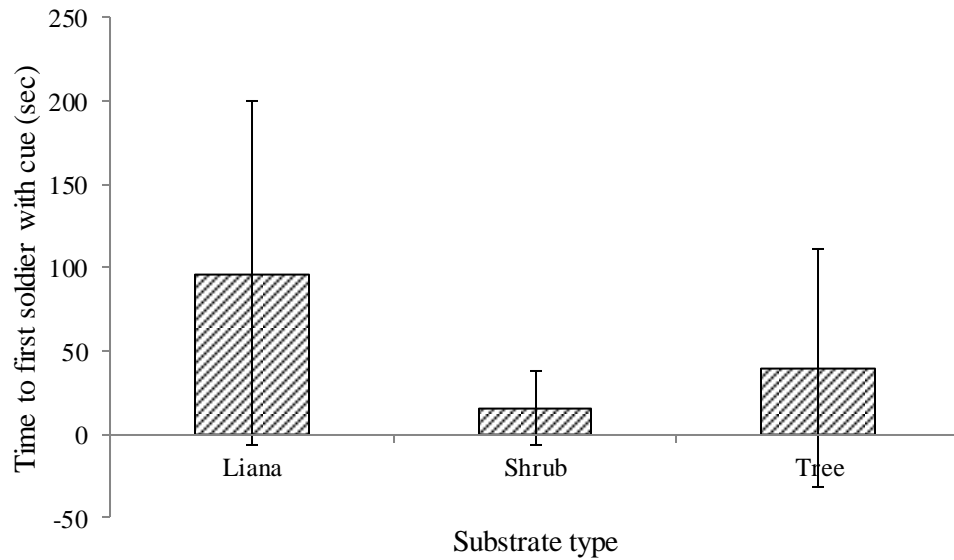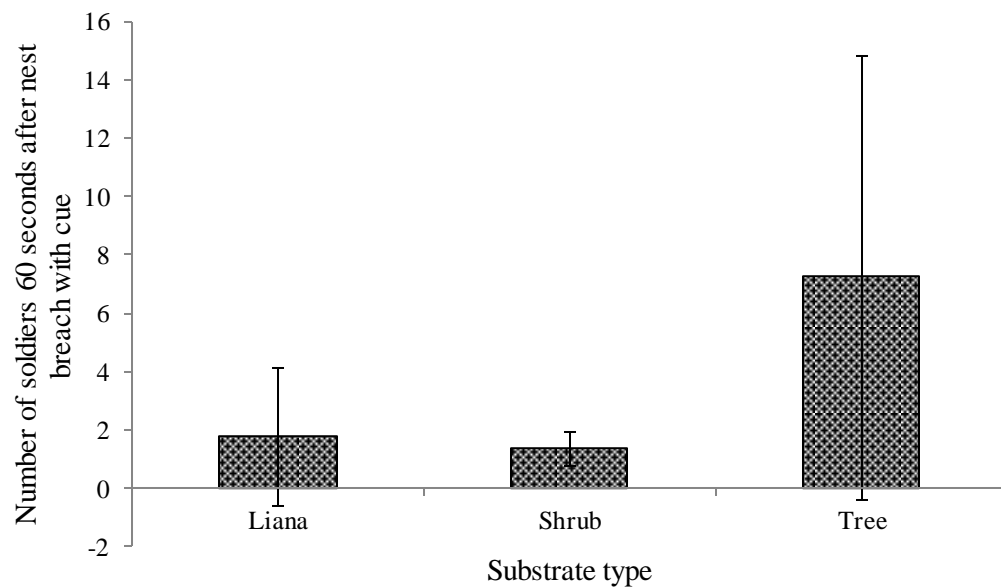

Figure 4: Number of soldiers present 60 seconds after nest breach for *Nasutitermes* spp. nests located in lianas, shrubs, and trees in trials without advanced cue at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.

Figure 5: Time to first soldier arrival after nest breach for *Nasutitermes* spp. nests located in lianas, shrubs, and trees in trials with advance cue at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.

Figure 6: Number of soldiers present 60 seconds after nest breach for *Nasutitermes* spp. nests located in lianas, shrubs, and trees in trials with advance cue at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.
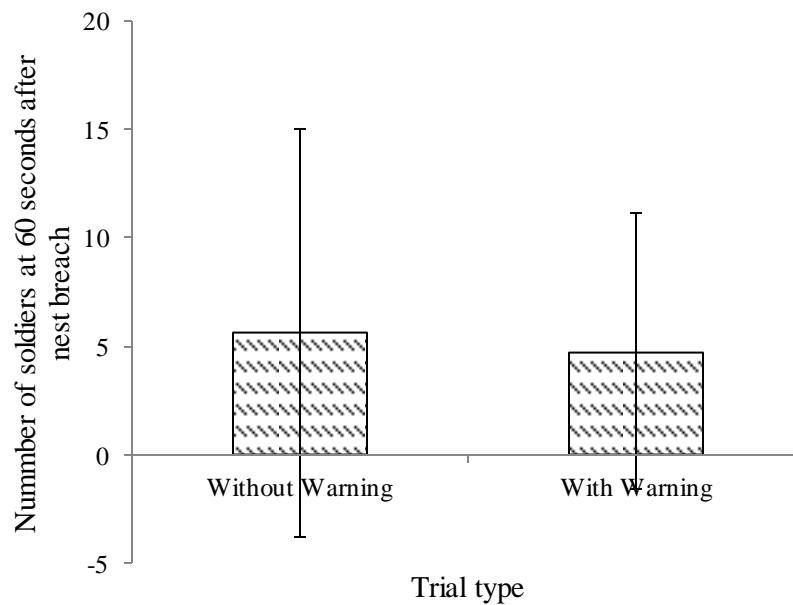
Figure 7: Number of soldiers present 60 seconds after nest breach for *Nasutitermes* spp. nests in trials with and without advance cue at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.
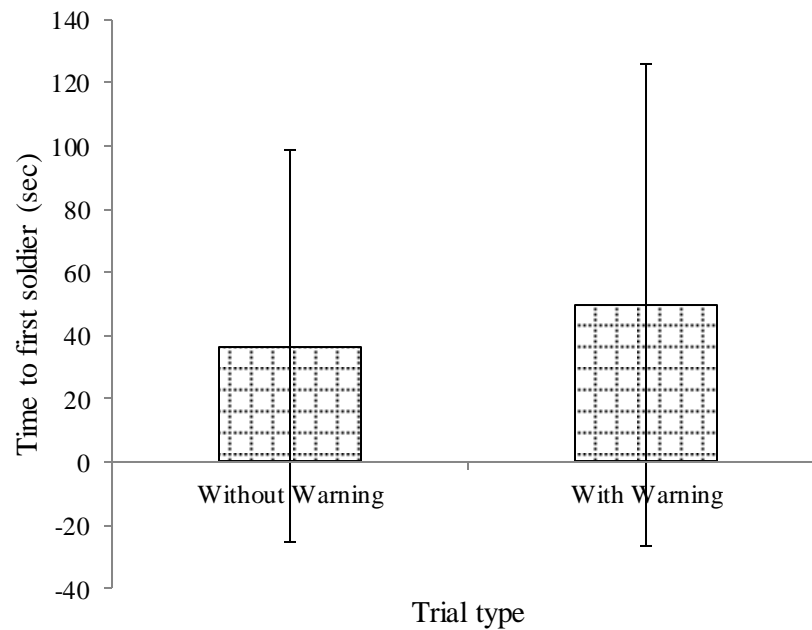

Figure 8: Time to first soldier's arrival after nest breach for *Nasutitermes* spp. nests in trials with and without advance cue at OTS Palo Verde Biological Station, Costa Rica. February-March 2013.