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RESEARCH ARTICLE - TERMITES

Survivorship of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae) in a Hypoxic Environment

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Abstract

The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, is a structural pest of major economic importance in the city of New Orleans, Louisiana. Hurricane Katrina made landfall along the United States Gulf coast on August 29, 2005, inundating approximately 80% of the city. Though termite colonies survived prolonged inundation, the survival mechanisms of colonies have yet to be fully understood. One hypothesis is that *C. formosanus* colonies survived within pockets of trapped air within their nesting system during this period of flooding. This hypothesis was tested by measuring mortality of groups of 20, 40, and 60 termites in airtight environments maintained at three different temperatures. Groups of 20 termites maintained at 10, 21, and 32°C reached 100% mortality at 89.5, 52.0, and 3.5 days, respectively. Groups of 40 termites maintained at 10, 21, and 32°C reached 100% mortality at 89.5, 51.0, and 3.5 days, respectively. Groups of 60 termites maintained at 10, 21, and 32°C yielded 100% mortality at 57.5, 22.5, and 1.0 day, respectively. Field colonies of *C. formosanus* established before Hurricane Katrina survived up to three weeks of flooding, and our findings suggest that it is possible for inundated colonies to survive this prolonged flooding by remaining within air pockets located in their nesting system until flood waters recede.

Introduction

The Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), is a structural pest of major economic importance that was introduced into New Orleans, Louisiana from southeastern China following World War II (La Fage, 1987). In New Orleans, *C. formosanus* populations are well-established and readily outcompete the native subterranean termites, *Reticulitermes* spp. (Isoptera: Rhinotermitidae), as the primary structural pest in the greater New Orleans area (Su, 2003). It has been suggested that the city of New Orleans has one of the highest termite pressures in North America (Lax & Osbrink, 2003).

Coptotermes formosanus is a cryptic species. It creates gallery systems as well as carton nests consisting of soil, wood, saliva, and frass below the soil surface, within trees, and inside tree stumps. Excavation of *C. formosanus* foraging galleries showed that branching subterranean galleries were connected to multiple nests consisting of cavities enclosed by carton material (King & Spink, 1969). *Coptotermes formosanus* readily infests live trees, creating voids and building carton material within them (La Fage, 1987; Osbrink et al., 1999). According to Osbrink et al. (1999), these nests can be located both under the soil surface or meters above the ground level within tree trunks.

On August 29, 2005, Hurricane Katrina made landfall along the United States Gulf coast. Subsequent levee breaches within New Orleans resulted in approximately 80% of the city being inundated (www.fema.gov). In some areas, flooding lasted up to three weeks. Cornelius et al. (2007) observed actively foraging termites within previously established in-ground monitoring stations that had been flooded for up to two weeks within months after the flood waters receded. Owens et al. (2012) confirmed that at least some *C. formosanus* colonies

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present at established research sites before inundation were the same as those present following inundation. Though termite colonies survived prolonged inundation, the survival mechanisms of colonies have yet to be fully understood.

Forschler and Henderson (1995) determined that the LT_{50} value for inundated *C. formosanus* workers was 11.1 hours, and the LT_{90} value was 15.8 hours. Field colonies of *C. formosanus* established before Hurricane Katrina survived up to three weeks of flooding, much longer than the survival capabilities observed of termites subjected to inundation bioassays. For *C. formosanus* colonies to survive this prolonged inundation, they must have had access to an oxygen source.

The hypothesis tested in the current study is that *C. formosanus* colonies could have survived the flooding following Hurricane Katrina by exploiting oxygen trapped within their nesting system. It has been suggested that survival of *C. formosanus* during prolonged inundation may be due to hydrophobic properties of carton material (Cornelius et al., 2007) and trapped air within voids of infested trees (Osbrink et al., 2008). The number of termites and temperature within the nesting system could have influenced termite survivorship during inundation as well. This is because the greater the number of termites confined to a space, the faster the available oxygen would be consumed for respiration. Temperature would have influenced survivorship, as termites exhibit increased respiration at relatively warmer temperatures (Cotton, 1932). Our objective was to determine if *C. formosanus* colonies could have survived the flooding following Hurricane Katrina by remaining in an airtight environment that contains a limited amount of oxygen for up to three weeks.

Materials and Methods

Termites

Termites were collected from three field colonies in New Orleans, Louisiana. The first field colony was located N 29.92372, W -90.13063, the second colony was located N 30.01825, W -90.09747, and the third colony was located N 30.03189, W -90.07253. Termites were collected from previously established milk crate traps (Kleinpeter Farms Dairy, Baton Rouge, LA) installed below the soil surface and filled with untreated pine (*Pinus* sp.) stakes (2 by 4 by 28 cm in length). Collected termites were transported and stored within corrugated cardboard moistened with distilled water in the laboratory at 24°C. Within one week, termites were bioassayed. Voucher specimens for all colonies were deposited in the NOMTCB's arthropod collection.

Termite Survivorship in an Airtight Environment

For each colony, there were three experimental groups and three control groups. The first group consisted of 20 termites per replicate, the second group consisted of 40 termites per replicate, and the third group consisted of 60 termites per replicate. Each group consisted of 10% soldiers and 90% workers (undifferentiated larvae of at least the third instar), which is consistent with the soldier ratio observed in established field colonies (Lax & Osbrink, 2003). Termites were maintained at three different temperatures: 10, 21, and 32°C. There were three replicates for each experimental and each control group for each temperature at which termites were maintained.

Bioassays were conducted within 9 ml glass vials, each containing 3 ml 3% agar to maintain moisture and two cylindrical pieces (2 mm diameter by 20 mm in length) of untreated wood as a food source. When the volumes of agar and wood resource were subtracted from the total volume of the vial, it was determined that the available air within each vial was 5.94 cm^3. Termites were added to their respective vials. The vials containing the experimental groups were topped with a screw cap and wrapped in Parafilm (Bemis, Neenah, WI) to create an airtight environment. These vials served to replicate an environment similar to what may be observed within a pocket of air inside the termite nesting system during times of flooding. The vials containing the control groups were topped with a piece of stainless steel mesh (2 by 2 cm) (Termimesh LLC, Austin, TX), which allowed for air circulation.

Mortality of termites maintained at 10 and 21°C was evaluated at 12 hour intervals until 100% mortality was reached. Termites maintained at 32°C were observed at 6 hour intervals for mortality. Data were corrected using Abbott's (1925) formula. Pooled data were analyzed by probit analysis to determine the lethal time, in days, for 50% (LT_{50}) and 90% (LT_{90}) of the test population for all groups of termites maintained at the three different temperatures. Mortality rates for groups of 20, 40, and 60 termites maintained at each temperature were compared to each other using analysis of variance (ANOVA) (PROC GLM) and Tukey's Honestly Significant Difference (HSD) test with a level of significance when $\alpha < 0.05$. Worker and soldier mortality rates at each temperature were compared using a paired *t*-test. Mortality data of all termites maintained at each temperature were pooled and compared to each other using ANOVA (PROC GLM). All statistical analyses were conducted using SAS 9.1 (SAS Institute, 2003, Cary, NC).

Results

Total mortality for all treatment groups was observed from 1.0 to 89.5 days, depending on temperature and the number of termites confined within each vial. Percent mortality for all groups of termites maintained at three different temperatures was plotted over time (Fig 1). Probit analysis on groups of 20, 40, and 60 termites confined within airtight vials and maintained at three different temperatures yielded LT_{50} values that ranged from 0.3 and 23.0 days (Table 1). Mortality of the control groups maintained at all three temperatures ranged from zero to 5%.

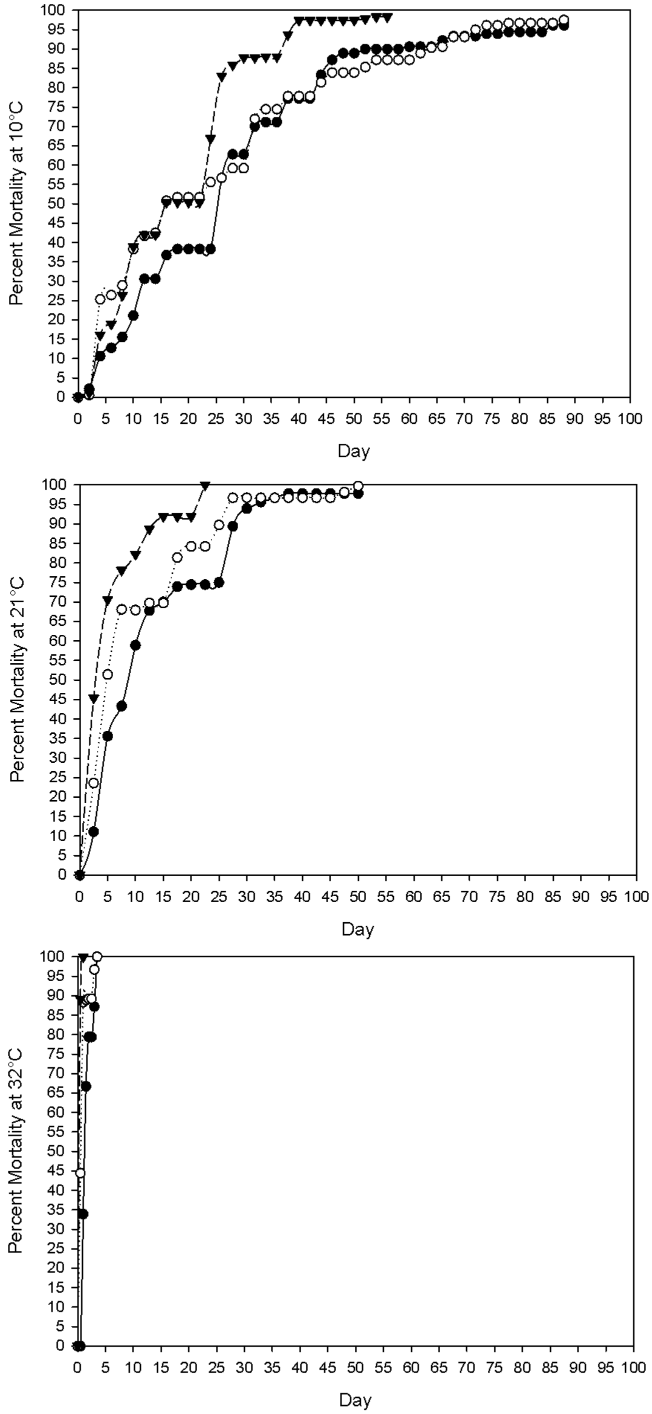

Fig 1. Percent mortality of termites maintained in an airtight environment at 10°C, 21°C, and 32°C plotted against time. Closed circles represent mortality of groups of 20 termites. Open circles represent mortality of groups of 40 termites. Triangles represent mortality of groups of 60 termites.

Mortality rates of groups of 20, 40, and 60 termites were significantly different at 10°C (F = 227.95, df = 2, P < 0.0001), 21°C (F = 125.57, df = 2, P < 0.0001), and 32°C (F = 7.86, df = 2, P < 0.0066). At 10 and 21°C, groups of 20 termites yielded the lowest mortality, while groups of 60 termites yielded the highest mortality. At 32°C, groups of 20 termites exhibited significantly lower mortality rates than that for groups of 60 termites, though mortality rates of groups of 40 termites were not significantly different than that of groups of 20 or 60 termites. Workers showed significantly lower mortality rates than soldiers at 10°C (t = -14.26, df = 178, P < 0.0001) and at 21°C (t = -6.6, df = 103, P < 0.0001). At 32°C, worker and soldier mortality rates were not significantly different (t = -0.70, df = 6, P = 0.5119).

Analysis of variance conducted on pooled mortality of all groups of termites at each temperature showed a significant difference between mortality rates of termites maintained at 10, 21 and 32°C (F = 143.6, df = 2, P < 0.0001). Termites maintained at 10°C exhibited significantly lower mortality than termites maintained at either 21 or 32°C. Termites maintained at 32°C exhibited significantly higher mortality than termites maintained at either 10 or 21°C.

Table 1. Comparison of lethal times, LT_{50}s and LT_{90}s (days), with their associated slopes, 95% CLs, and Pearson X^2 values from groups of 20, 40, and 60 *C. formosanus* confined to an airtight environment and maintained at three different temperatures.

Temp	No. of termites	n	slope ± SE	LT_{50}	95% CL	LT_{90}	95% CL	X^2 (df)	P
10	20	32,220	2.98 ± 0.07	23.00	22.01 – 23.96	61.89	60.22 – 63.69	372.14 (176)	<0.0001
	40	64,440	2.51 ± 0.12	20.31	18.06 – 22.43	65.96	63.41 – 68.71	921.64 (176)	<0.0001
	60	62,100	3.91 ± 0.21	16.80	15.44 – 18.02	35.71	34.27 – 37.32	1,505.76 (112)	<0.0001
21	20	18,720	2.19 ± 0.10	6.99	5.92 – 8.06	26.82	24.44 – 29.46	650.10 (101)	<0.0001
	40	36,720	1.88 ± 0.07	4.41	3.70 – 5.14	21.18	19.19 – 23.34	768.66 (99)	<0.0001
	60	24,300	1.51 ± 0.08	1.92	1.47 – 2.42	13.56	11.63 – 15.83	313.02 (42)	<0.0001
32	20	1,260	3.53 ± 0.70	1.14	0.57 – 1.71	2.64	1.76 – 6.11	57.61 (4)	<0.0001
	40	2,520	2.14 ± 0.62	0.43	0.0003 – 1.28	1.70	0.16 – 5.71	79.45 (4)	<0.0001
	60	2,160	3.94 ± 0.69	0.27	0.07 – 0.38	0.57	0.39 – 2.02	29.40 (2)	<0.0001

Discussion

Significant differences of mortality rates between the experimental groups of termites confined within an airtight environment showed that the greater the ratio of available air space to the number of termites confined to that space, the greater the survivorship. At 10 and 21°C, groups of 20 termites, when compared to groups of 40 and 60 termites, survived for a significantly longer period. This was also observed for groups of 20 termites when compared to groups of 60 termites at 32°C. Higher mortality for groups of 40 or 60 termites may be due to more termites consuming the available oxygen causing a lack of available oxygen, or from increasing levels of carbon dioxide produced through respiration.

It was expected that soldiers would experience lower mortality rates than workers in a hypoxic environment. This is because workers pursue various tasks, including tunneling and feeding, thus expending more energy and increasing their oxygen requirements. However, our results showed otherwise. At 10 and 21°C, workers survived significantly longer than soldiers. At 32°C, no such difference between worker and soldier mortality was observed.

It was also speculated that termites maintained at relatively lower temperatures would survive for longer periods than those maintained at relatively higher temperatures. This is because increased respiration by termites at relatively warmer temperatures reflects an increase of oxygen required by termites for metabolic activity (Cotton, 1932). Furthermore, it is known that termite physical activities such as foraging and wood consumption increase during months of relatively warmer air and soil temperature (Fei & Henderson, 2004; Messenger and Su, 2005; Cornelius and Osbrink, 2011; Delaplane et al., 1991). Results of this study confirmed our speculation.

According to the data presented here, 50% of a group of 20 termites (i.e. 10 termites) can survive being confined to approximately 6 cm^3 of air space for 23 days at 10°C, 7 days at 21°C, and 1 day at 32°C. Ten percent of a group of 20 termites (i.e. two termites) can survive in this same space for almost 62 days at 10°C, 27 days at 21°C, and 3 days at 32°C. According to figures by Cornelius and Osbrink (2011), soil temperatures in New Orleans, Louisiana ranged from 25 to 35°C between July and October for two consecutive yrs. The temperature of saturated soil during the flooding that followed Hurricane Katrina is unknown, but it is possible that flood conditions reduced the soil temperature. Therefore, termites inundated following the hurricane would likely be represented by workers and soldiers bioassayed at 21 and 32°C. Between the temperatures of 32 and 21°C, the LT_{50}s ranged from 1 to 7 days for 20 termites in a hypoxic environment. At these same temperatures, the LT_{90}s ranged from 3 to 27 days. If the soil temperatures were lowered below 21°C during this flood event, termites within their nesting system could have survived for an even longer period.

When considering subterranean termite colony mortality due to treatment, or in this case a flood event which may confine termites within pockets of air, the colony itself must be considered as a unit, rather than placing focus solely on the mortality of individual termites. Even if only a portion of a colony survives, the colony itself may eventually recover, when more foragers and reproductives are produced (Su & Scheffrahn, 1990). A study of *C. formosanus* field colonies within City Park revealed an initial reduction of *C. formosanus* populations after being inundated for more than two weeks (Osbrink et al., 2008). However, this study showed populations rebounded the following year. This is indicative of a colony that experienced loss of individual termites due to inundation, but continued to produce foragers and increase its colony size.

The LT_{90}s derived from our data show that 10% of the test population can survive in approximately 6 cm^3 of available air up to 27 days (3.8 weeks) at 21°C, which is longer than the two to three week inundation duration observed after Hurricane Katrina. During the flooding that followed Hurricane Katrina, termites not succumbed to rising water may have survived by remaining in pockets of air within their hydrophobic carton material. *Coptotermes formosanus* readily builds carton nests within live trees and under the soil surface (Osbrink et al., 1999). A study conducted by Cornelius and Osbrink (2010) revealed that termites allowed to live and feed within hollowed wood blocks were able to survive inundation as long as they were located within the hollowed core at the time of flooding. This is also indicative of termite colonies being able to survive by exploiting air pockets within their nesting system.

Whether *C. formosanus* survived inundation by this mechanism remains unknown, as carton material within tree voids and structures could not be observed during flooding. However, groups of termites can survive more than three weeks within an airtight environment, depending on temperature and the ratio of available space to the number of termites confined to that space. Furthermore, *C. formosanus* individuals exist within subterranean nests and experience relatively low O_2 and high CO_2 concentrations and are capable of slightly reducing their respiration rates in these environments (Wheeler et al., 1996). This would also contribute to their survival capabilities in a hypoxic environment during times of flooding.

Survival mechanisms of insects inhabiting hypoxic environments vary. Several species of insects reduce their metabolic rates and become quiescent when exposed to hypoxic environments. For example, intertidal root aphids, *Pemphigus trehernei* Foster, become quiescent when submerged (Hoback & Stanley, 2001). Tiger beetle larvae of the species *Cicindela togata* Laferte reduce their metabolic rates to survive repeated flooding of their larval habitat along flood plains (Hoback et al., 1998).

Based on our findings, the hypothesis that *C. formosanus* colonies can survive flooding by exploiting trapped air is accepted. It would be possible for inundated termites to survive the flooding following Hurricane Katrina by remaining within air pockets located in their nesting system until flood waters receded, but only if their nesting system was sealed and provided sufficient protection from being filled with water.

It is important to understand the capability of *C. formosanus* to survive flood conditions, which are not only city-wide and caused by natural disasters, but are more regularly localized within the city and caused by heavy rainfall. Homeowners and individuals within the pest control community should understand that prolonged inundation will not eliminate *C. formosanus* colonies.

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