# Survival of termites (Isoptera) exposed to various levels of relative humidity (RH) and water availability, and their RH preferences

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**Abstract**

Termites (Isoptera) are widely believed to be one of the most desiccation-prone insects. They must combat desiccation by locating and efficiently conserving water resources. Termites have evolved morphological, physiological, and behavioral characteristics that aid in the tolerance of desiccation. In 3 studies using 4 termite species, water loss tolerance and relative humidity (RH) preferences of termites exposed to 5 different RH, as well as the use of different water sources, were examined. Our results showed that *Coptotermes formosanus* Shiraki (Rhinotermitidae) preferred and survived better at high RH and with readily available water sources. *Neotermes jouteli* (Banks in Banks and Snyder) (Kalotermitidae) also preferred a high RH, but was more capable of tolerating lower RH and a lack of free water than *C. formosanus*. *Cryptotermes brevis* Walker (Kalotermitidae) and *Cryptotermes cavifrons* Banks (Kalotermitidae) did not exhibit greater survival in a certain RH nor when exposed to various sources of water. These two species also did not exhibit a preference for a certain RH.

Key Words: dampwood termite; desiccation; drywood termite; huddling; subterranean termite

**Resumen**

Se cree que las termitas (Isoptera) son uno de los insectos más propensos a la desecación. Deben combatir la desecación mediante la localización y conservación eficiente de los recursos hídricos. Las termitas han desarrollado características morfológicas, fisiológicas y de comportamiento que ayudan en la tolerancia a la desecación. En 3 estudios con 4 especies de termitas, se examinaron las preferencias de tolerancia a la pérdida de agua y de humedad relativa (RH) de las termitas expuestas a 5 diferentes RH, así como el uso de diferentes fuentes de agua. Nuestros resultados mostraron que *Coptotermes formosanus* Shiraki (Rhinotermitidae) prefirió y sobrevivió mejor a alto RH y con fuentes de agua fácilmente disponibles. *Neotermes jouteli* (Banks en Banks & Snyder) (Kalotermitidae) también prefirió un RH alto, pero fue más capaz de tolerar un RH más bajo y una falta de agua libre que *C. formosanus*. *Cryptotermes brevis* Walker (Kalotermitidae) y *Cryptotermes cavifrons* Banks (Kalotermitidae) no mostraron mayor supervivencia en un cierto RH ni cuando se expusieron a diversas fuentes de agua. Estas dos especies tampoco mostraron preferencia por un HR determinado.

Palabras Clave: termitas de humedad; desecación; termitas de madera seca; acurrucamiento termitas subterráneas

Due to their small size and relatively unsclerotized body, water loss is a common problem facing all termite species, and they must locate and utilize water resources to prevent or tolerate desiccation. Water resources may be found as free water, moist food, or moist soil. Termites live in various habitats and microhabitats with differing levels of ambient humidity and availability of water, and water management among termite species has been the subject of many studies (Collins 1958, 1963, 1966, 1969; Abushama 1974; Rust et al. 1979; Steward 1983; Sponsler & Appel 1990; Rudolph et al. 1990; Grube & Rudolph 1999a, 1999b; Gallagher & Jones 2010; Gautam & Henderson 2014). Some kalotermitid termites exhibit behavior and impacts on survival that indicate that high humidity is toxic to them (Collins 1969; Minnick et al. 1973; Steward 1982, 1983; Rudolph et al. 1990; Woodrow et al. 2000). Strickland (1950), Collins (1958, 1969, 1991), and Khan (1980), found that different termite species can tolerate various (sometimes extreme) humidity and temperature conditions; however, there are undoubtedly conditions that termites prefer over other conditions that they can tolerate.

The first objective of this study was to investigate the survivorship of 4 termite (Isoptera) species that inhabit distinctly different microhabitats, including *Coptotermes formosanus* Shiraki (Rhinotermitidae), *Neotermes jouteli* (Banks in Banks and Snyder) (Kalotermitidae), *Cryptotermes brevis* Walker (Kalotermitidae), and *Cryptoterme cavifrons* Banks (Kalotermitidae). *Coptotermes formosanus* and *N. jouteli* live in high relative humidity (RH) environments, whereas *Cr. brevis* is found in dry timber and *Cr. cavifrons* is found in natural wood that can be wet or dry.

The second objective of this study was to investigate the RH preferences of the aforementioned species. Humidity is not the only water source available to termites. There are other water sources that termites might use. These include metabolic water obtained through the breakdown of food, from the fat body, free liquid water, as well as water bound to various substrates (e.g., wood, soil, and nestmate cadavers). Different termite species (i.e., drywood, dampwood, subterranean) use or avoid certain environments with different moisture and water sources. Whereas drywood termites depend heavily on metabolically derived water, dampwood and subterranean termites that live in high RH environments obtain water from their surroundings (Lee & Wood 1971, Brammer & Scheffrahn 2007, Scheffrahn & Su 2007). The third objective of this study was to investigate whether these 4 termite species use a variety of water sources for survival.

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## Materials and Methods

### INSECT COLONIES

Individuals from colonies of *C. formosanus*, *N. jouteli, Cr. cavifrons,* and *Cr. brevis* were collected in Broward County, Florida. Different colonies of *C. formosanus* were collected from bucket traps as described by Su and Scheffrahn (1986). Colonies of *N. jouteli, Cr. cavifrons,* and *Cr. brevis* were collected from different pieces of wood. *Coptotermes formosanus* and *N. jouteli* were kept in polystyrene boxes (17.15 × 12.22 × 6.03 cm) with wood (*Pinus* sp.) maintained at 26.4 °C, and were regularly misted with water to maintain >95% RH. *Cryptotermes* termites were kept in polystyrene boxes with wood pieces and stored in the incubator (26.4 °C and 41.5% RH). For *Cr. cavifrons,* small dishes with water were provided. Populations of each termite species survived well in these conditions and were used for experiments as needed. Termites were kept in the incubator for <6 mo before use.

### TERMITE SURVIVORSHIP AT VARIOUS RELATIVE HUMIDITIES

Desiccative humidity chambers consisted of clear polystyrene boxes (17.15 × 12.22 × 6.03 cm) with internal RH conditions stabilized using three saturated salt solutions (i.e., NaCl, $Mg(NO_3)_2$, and $MgCl_2$), silica gel, and water (Fig. 1A) as described by Rockland (1960), and Winston and Bates (1960). Open Petri dishes (93 mm diameter, 22 mm height) containing water or 1 of the saturated salt solutions were placed at the center of 4 chambers (Fig. 1A, a–d), while silica gel was placed on the bottom of the chamber (Fig. 1A, e) to produce the lowest RH. The container edge was coated with petroleum jelly (Eboneen Products Company, Inc., Hartford, Connecticut) to create a seal between the lid and chamber. Temperature and humidity levels were measured daily using a probe (THW3; Amprobe, Everett, Washington) (Fig. 1B, i) through an access hole (1.59 cm diameter) in the lid. These holes were plugged with rubber stoppers while not in use (Fig. 1B, h). The average RH (± standard error of the mean [SEM]) of the chambers and their associated stabilizing material were as follows ($n$ = 73): 92.0 ± 0.07% ($H_2O$), 72.9 ± 0.08% (NaCl), 55.7 ± 0.09% ($Mg(NO_3)_2$), 34.3 ± 0.04% ($MgCl_2$), and 18.2 ± 0.14% (silica gel). The average temperature (± SEM) of the chambers and their associated stabilizing material were as follows ($n$ = 73): 23.5 ± 0.06 °C ($H_2O$), 23.6 ± 0.06 °C (NaCl), 23.5 ± 0.06 °C ($Mg(NO_3)_2$), 23.7 ± 0.06 °C ($MgCl_2$), and 23.6 ± 0.06 °C (silica gel). Groups of 10 termite individuals per species were placed in the Petri dish (35 mm diameter, 10 mm height) of each chamber with small holes cut into the lids of the dishes to allow air movement and yet prevent termite escape. Dishes were also provisioned with a small (15 × 15 × 9 mm) piece of wood (*Pinus* sp.) as a food source. Four dishes, each containing 1 of the 4 termite species, were placed in the humidity chamber surrounding water or salt solutions (Fig. 1A, a–d), or on top of the silica gel in a chamber (Fig. 1A, e).

Temperature and humidity readings were recorded every 24 h post-introduction for 12 d. Daily counts of live termites were recorded for a 12 d period. A follow-up experiment also was conducted to examine recovery of *N. jouteli* individuals that exhibited visible reduction in body mass. At the conclusion of the 12 d study, the surviving *N. jouteli* individuals from the various RH were weighed and then placed in a Petri dish and provided with food and water for 1 wk. Surviving termites were counted and weighed again to examine recovery when provided with adequate food and water resources.

Statistical analysis was carried out using JMP statistical software (SAS 2015). An analysis of variance (ANOVA) for a 4 by 5 factorial experimental design was conducted to test for differences. Termite species (4) and RH (5) were the factors, and percentage survival was the response variable. Percentage survival values were arcsine-square root transformed before analysis. Post hoc Tukey honest significant difference tests were used to evaluate all pairwise differences at $\alpha$ = 0.05. Data from 6 replicates were analyzed.

### TERMITE PREFERENCE FOR VARIOUS RELATIVE HUMIDITIES

Multiple-choice arenas were constructed by connecting a central chamber (89 mL [3 oz] clear plastic jars, 52 mm diameter, 53 mm height) with four radial chambers (Fig. 2A). Drierite (W.A. Hammond DRIERITE Co. Ltd., Xenia, Ohio) was used for the central chamber, whereas water, NaCl, $Mg(NO_3)_2$, and $MgCl_2$ were used for the 4 radial chambers to maintain desired RH. The average ($n$ = 21) RH (± SEM) of the chambers and their associated stabilizing material were as follows: 90.7 ± 0.24% ($H_2O$), 71.7 ± 0.20% (NaCl), 52.0 ± 0.12% ($Mg(NO_3)_2$), 34.1 ± 0.16% ($MgCl_2$), and 8.4 ± 0.48% (Drierite). The average ($n$ = 21) temperature (± SEM) of the chambers and their associated stabilizing material were as follows: 23.4 ± 0.06 °C ($H_2O$), 23.5 ± 0.06 °C (NaCl), 23.4 ± 0.06 °C ($Mg(NO_3)_2$), 23.4 ± 0.06 °C ($MgCl_2$), and 23.4 ± 0.05 °C (Drierite). A temperature and humidity probe was inserted through access holes (1.59 cm diameter) in the lids to take measurements inside the chambers as described previously (Fig. 2A, b). Relative humidity stabilizing solutions or materials were placed in the bottom of the jar chambers (Fig. 2B).

Chambers housed modified plastic vials (25 mm inner diameter, 15 mm height) cut to hold the termites while preventing their escape (Fig. 2C, k). A hole (6 mm diameter) was drilled into the wall of each of the 4 radial chambers (2.5 cm from base) to allow pieces of plastic tubing (5.5 mm diameter, 50.0 mm length) (Fig. 2C, j) to connect radial termite vials to the vial in the central chamber. All termite vials were suspended by plastic tubes above the stabilizing materials. Groups of 25 pseudergates were placed into the introduction chamber for the larger sized species *N. jouteli*, while 50 termites (pseudergates and workers) were used for the other 3 smaller sized species.

Termites could move and acclimate to any chamber for 12 to 16 h. Black satin cloth covered the arenas to provide darkness. Counts of termites within each chamber were then recorded. Termites found in the connecting tubes were included in the counts for the connected chamber. Statistical analysis was conducted using JMP statistical software (SAS 2015). A 4 by 5 factorial analysis was conducted with termite species (4) and RH (5) as the factors and percentage of termites found in a chamber as the response variable. The percentage values were arcsine-square root transformed before the analysis of variance (ANOVA) was used to test whether there was a significant difference among RH preference for the 4 species. Post hoc Tukey honest significant difference tests were used to separate the differences for all pairs at $\alpha$ = 0.05. Data from 6 replications were analyzed.

### TERMITE SURVIVORSHIP WITH VARIOUS TYPES OF WATER SOURCES

Experimental chambers were constructed using clear plastic jars (52 mm diameter, 53 mm height) with plastic lids and lid liners. The bottoms of these jars were scratched with sandpaper to provide traction for termite movement. Temperature and humidity levels inside the jars were measured as described previously.

Five chambers that provided various sources of water, or the lack thereof, were used for the experiment. These included: chambers with a piece of dry wood (*Pinus* sp.; 18 × 18 × 8 mm), a piece of dry wood with a humidity source (i.e., a 2 × 6 cm wetted filter paper strips attached to the upper inner side of the chamber), a piece of wet wood, a piece of dry wood with wet sandy soil (5 g sand + 1.5 mL deionized water), and a piece of dry wood with a source of free

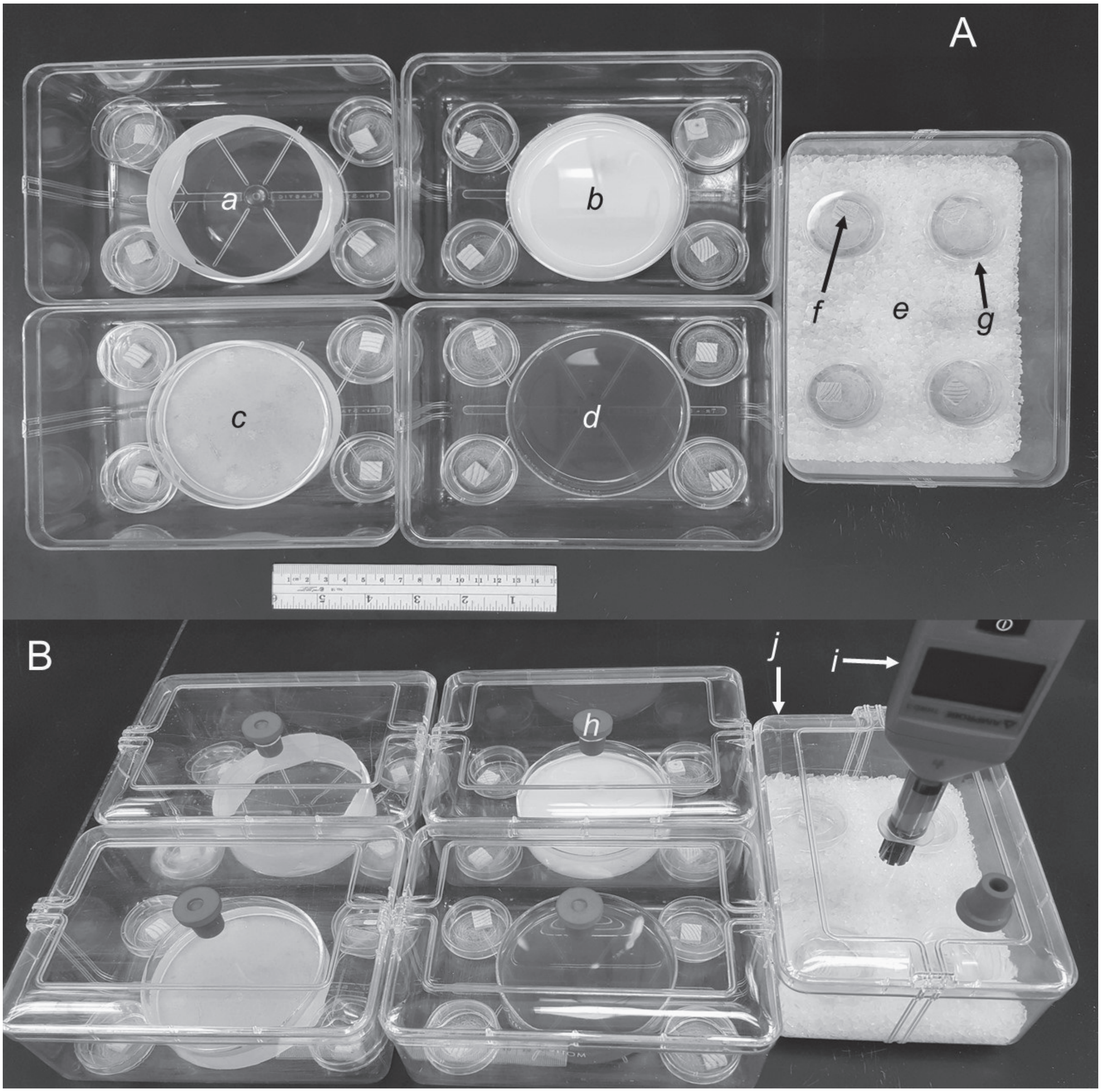


**Fig. 1.** Experimental units to examine termite survival when exposed to various relative humidity (RH) levels: A) Humidity chambers with lids removed: *a*: $H_2O$ dish with filter paper ring (92.0 ± 0.07% RH); *b*: NaCl dish (72.9 ± 0.08% RH); *c*: $Mg(NO_3)_2$ dish (55.7 ± 0.09% RH); d: $MgCl_2$ dish (34.3 ± 0.04% RH); *e*: silica gel layer (18.2 ± 0.14% RH); *f*: wood food source; *g*: holding dish with modified lid. B) Humidity chambers with lids in place: *h*: rubber stopper; *i*: temperature/humidity probe; *j*: chamber lid.

water in a small dish (modified shell vial cap, 15 mm diameter, 3 mm height). Water was added as needed to maintain RH and free water levels. The average ($n$ = 48) RH (± SEM) of the chambers and their associated water sources were as follows: 91.0 ± 0.22% (wet wood), 49.6 ± 0.61% (dry wood), 92.6 ± 0.22% (wet soil), 91.1 ± 0.22% (wood + water), and 94.2 ± 0.18% (wood + RH). The average ($n$ = 48) temperature (± SEM) of the chambers and their associated water sources were as follows: 24.2 ± 0.08 °C (wet wood), 24.1 ± 0.08 °C (dry wood), 24.2 ± 0.07 °C (wet soil), 24.2 ± 0.07 °C (wood + water), and 23.0 ± 0.03 °C (wood + RH).

Three sets of each of the chambers were broken down weekly for 4 wk to record termite survival for each species using destructive sampling. The data were analyzed using JMP statistical software (SAS 2015) and a 4 by 5 factorial experimental design with termite species (4) and water source (5) as the factors, and percentage survival as the response variable. Percentage survival data were arcsine square root transformed before analysis. Weekly data were analyzed separately. ANOVA was conducted to test for significant differences and post hoc Tukey honest significant difference tests were used to separate the differences for all pairs at α = 0.05. Data from 3 replications were analyzed.

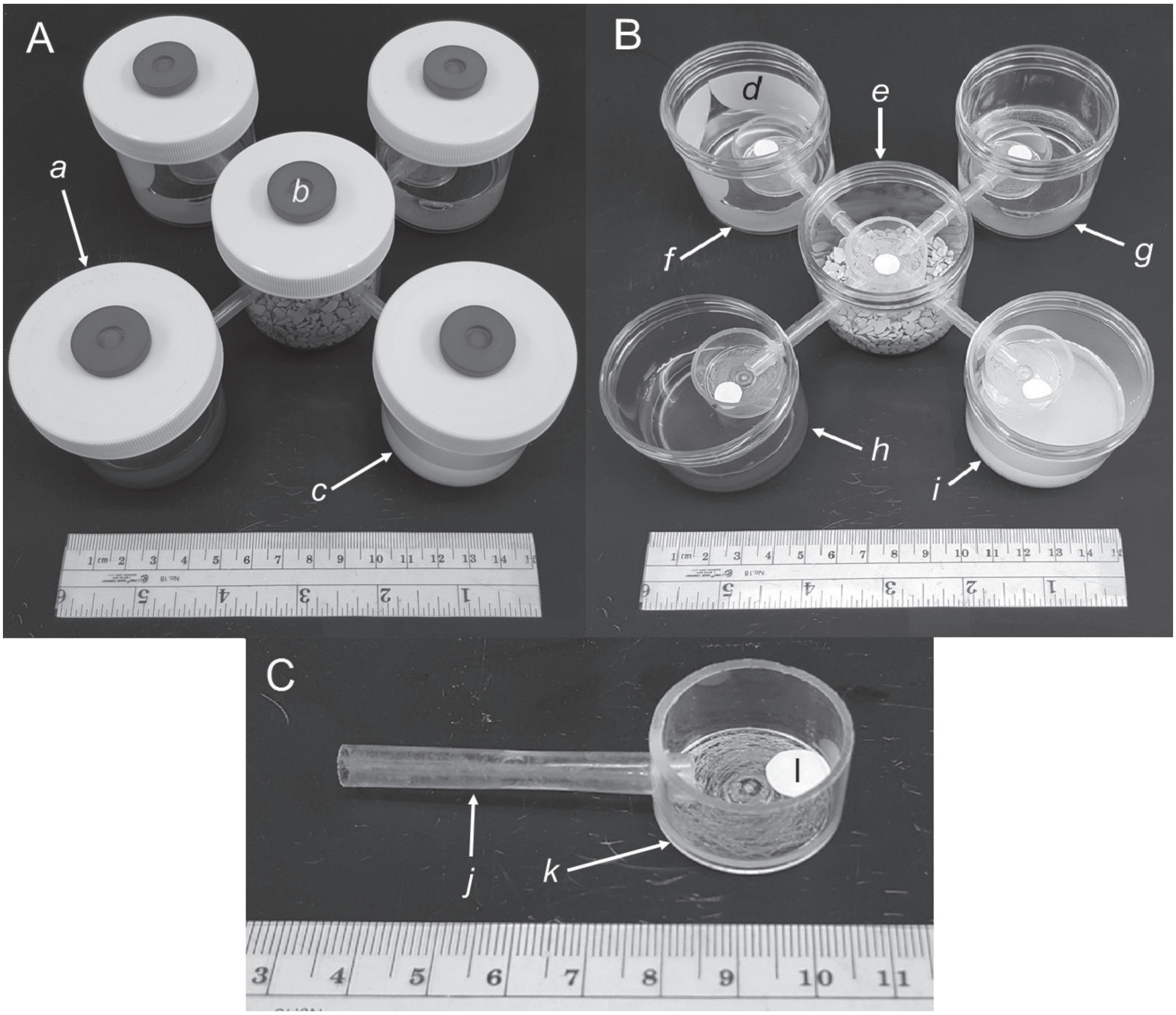


**Fig. 2.** Materials for determining relative humidity (RH) level preferences of four termite species. A) Arena with chamber lids in place: *a*: chamber lid; *b*: rubber stopper; *c*: jar chamber. B) Arena with chamber lids removed: *d*: filter paper semicircle; *e*: Drierite introduction chamber; *f*: $H_2O$ chamber; *g*: $MgCl_2$ camber; *h*: $Mg(NO_3)_2$ chamber; *i*: NaCl chamber. C) Close-up of arena components housing termites: *j*: connecting tube; *k*: holding dish; *l*: filter paper food source.

## Results

### TERMITE SURVIVORSHIP AT VARIOUS RELATIVE HUMIDITIES

Termites displayed statistically different responses to RH ($F$ = 90.0; df = 3, 116; $P$ <0.001). There was no significant difference in survival at any RH (18.2–92.0%) for *Cr. cavifrons*, *Cr. brevis*, and *N. jouteli*, but there was a significant difference for *C. formosanus*. This species survived at 92.0% RH, but died within a few days when maintained at ≤72.9% RH (Table 1). However, *N. jouteli* individuals in all the humidity chambers (18.2–72.9% RH) except the water chamber (92.0% RH) were visibly smaller at the end of the experiment than at the start. The *Cryptotermes* species did not exhibit this change in size. At 18.2 to 72.9% RH levels, *N. jouteli* groups decreased in mass (4.4–151.2 mg loss per 10 termites). Of the 180 *N. jouteli* individuals that survived at the various RH and were then placed in a dish and provided with food and water, 172 recovered. These 172 individuals exhibited a total weight gain of approximately 327 mg. The remaining 8 individuals were not accounted for, indicating they may have been cannibalized by nestmates as a food and water source. The *N. jouteli* groups of 10 individuals exhibited a decrease in mass of approximately 42.0% of their weight, either due to the loss of body water or body fat.

### TERMITE PREFERENCE FOR VARIOUS RELATIVE HUMIDITIES

Termites displayed statistically different responses to RH ($F$ = 7.06; df =3, 116; $P$ <0.001). The wetwood (nests in wood or soil high in moisture) species of *C. formosanus* and *N. jouteli* preferred the highest RH of 90.7% RH, which was significantly more than *Cr. cavifrons* and *Cr. brevis* and significantly more than the other RH (Table 2). The *Cryptotermes* species did not exhibit a preference for any RH when compared among species and among RH.

**Table 1.** Percentage of survival (mean ± standard error of the mean [SEM]) of 4 termite species (*Coptotermes formosanus, Neotermes jouteli, Cryptotermes brevis,* and *Cryptotermes cavifrons*) exposed to 5 RH and 23 °C for 12 d.

| | RH[abc] | | | | | |
|---|---|---|---|---|---|---|
| Species | $H_2O$ (92.0 ± 0.07%) | NaCl (72.9 ± 0.08%) | $Mg(NO_3)_2$ (55.7 ± 0.09%) | $MgCl_2$ (34.3 ± 0.04%) | Silica gel (18.2 ± 0.17%) | Mean species survival[d] |
| *C. formosanus* | 100 ± 0.0Aa | 0 .0 ± 0.0Ab | 0.0 ± 0.0Ab | 0.0 ± 0.0Ab | 0.0 ± 0.0Ab | 20.0 ± 7.4A |
| *N. jouteli* | 98.3 ± 1.7Aa | 100 ± 0.0Ba | 96.7 ± 2.1Ba | 95.0 ± 3.4Ba | 98.3 ± 1.7Ba | 97.7 ± 0.9B |
| *Cr. cavifrons* | 98.3 ± 1.7Aa | 100 ± 0.0Ba | 96.7 ± 2.1Ba | 98.3 ± 1.7Ba | 90.0 ± 6.3Ba | 96.7 ± 1.5B |
| *Cr. brevis* | 95.0 ± 2.2Aa | 93.3 ± 4.9Ba | 96.7 ± 5.4Ba | 96.7 ± 2.1Ba | 91.7 ± 4.0Ba | 93.7 ± 1.7B |
| Mean survival at RH[d] | 97.9 ± 0.8a | 73.3 ± 8.9b | 71.3 ± 8.7b | 72.5 ± 8.8b | 70.0 ± 8.6b | |

[a]Means followed by the same lowercase letters within a row or means followed by the same capital letter within a column are not significantly different at the α = 0.05 level (Tukey honest significant difference test).
[b]Value for the combination (species × RH) of treatments are means of 6 observations.
[c]Mean RH ± SEM produced by water, 3 salts, and silica gel are found in parentheses.
[d]Values for each main treatment effect (species, RH) are means of 30 and 24 observations, respectively.

### TERMITE SURVIVORSHIP WITH VARIOUS TYPES OF WATER SOURCES

Termites displayed statistically different responses to RH for wk 1 ($F$ = 5.71; df = 3, 56; $P$ <0.001), wk 2 ($F$ = 3.30; df = 3, 56; $P$ <0.001), wk 3 ($F$ = 3.89; df = 3, 56; $P$ <0.001), and wk 4 ($F$ = 4.91; df = 3, 56; $P$ <0.001). Within a week, none of the *C. formosanus* individuals survived in the chambers provisioned with a piece of dry wood at RH <49.6%. Survival of *C. formosanus* was significantly lower in the dry wood chamber when compared to the other 3 species at all weeks. They survived significantly better throughout the 4 wk experiment when provided with some form of water at RH >90% (Table 3) when compared to the low humidity of the dry wood chamber. The only exception was the low survivorship of 33.3% when *C. formosanus* was provided with a piece of dry wood and free water at 91.1% RH for 4 wk. Because of the high survivorship of 96.7% at 4 wk when provided with dry wood at a slightly elevated RH (94.2%), the low 33.3% survivorship may be attributed to other factors such as handling. In the first 3 weeks, survival was not significantly different for *N. jouteli, Cr. Brevis,* and *Cr. cavifrons* when compared between the 5 water source chambers, as well as when compared with each other. After 4 wk, survival of *C. formosanus* exposed to dry wood was significantly lower when compared to wet wood, wet soil, and wood with a RH source. *Cryptotermes brevis* also exhibited significantly lower survival with wet wood when compared to *C. formosanus,* and wood with a RH source when compared to *Cr. cavifrons* (Table 3).

## Discussion

Results of this study showed that *C. formosanus* is less capable of tolerating desiccation than *N. jouteli*, *Cr. cavifrons*, or *Cr. brevis*. This agrees with previous studies of Collins (1958, 1963, 1966, 1969) and Khan (1980) on Kalotermitidae and Rhinotermitidae species. *Neotermes jouteli* did not express a difference in survival at the various RH, but lost body mass while remaining alive, most likely due to the need to generate metabolic water from reserve body fat, and exhibited a reduction in movement at RH below 72.9%.

The *Cryptotermes* species did not show a difference in survival when compared at the 5 RH of the first objective and did not exhibit a change in behavior. The physiological mechanisms involved in desiccation tolerance remain to be elucidated, but are probably related to cuticular permeability and percentage of total body water.

The results illustrate the necessity for *C. formosanus*, and preference of *N. jouteli*, to inhabit environments with high levels of moisture. *Coptotermes formosanus*, a subterranean species, not only requires high RH, but also other sources of water for normal activity and survival (Gautam & Henderson 2011). Tunneling activity of *Coptotermes gestroi* (Wasmann) (Rhinotermitidae), *Heterotermes tenuis* (Hagen) (Rhinotermitidae), *C. formosanus*, and *Reticulitermes flavipes* (Kollar) (Rhinotermitidae) in studies by Arab and Costa-Leonardo (2005) and Su and Puche (2003), showed that these species tunneled more in substrates with higher moisture content. Additionally, the effect of substrate and food moisture levels on survival, consumption, and

**Table 2.** Relative humidity (RH) (mean ± standard error of the mean [SEM]) preference of 4 termite species (*Coptotermes formosanus, Neotermes jouteli, Cryptotermes brevis,* and *Cryptotermes cavifrons*) expressed as the percentage of individuals found at each RH level.

| | RH[abc] | | | | |
|---|---|---|---|---|---|
| Species | $H_2O$ (90.7 ± 0.24%) | NaCl (71.7 ± 0.20%) | $Mg(NO_3)_2$ (52.0 ± 0.12%) | $MgCl_2$ (34.1 ± 0.16%) | Drierite (8.4 ± 0.48%) |
| *C. formosanus* | 89.3 ± 2.5Aa | 4.00 ± 1.5Ab | 3.30 ± 1.4Ab | 2.00 ± 0.9Ab | 1.3 ± 0.8Ab |
| *N. jouteli* | 91.3 ± 2.8Aa | 4.70 ± 1.2Ab | 3.30 ± 2.6Ab | 0.70 ± 0.7Ab | 0.0 ± 0.0Ab |
| *Cr. cavifrons* | 18.3 ± 16.4Ba | 42.3 ± 19.0Aa | 1.00 ± 1.0Aa | 21.0 ± 13.2Aa | 17.3 ± 8.8Aa |
| *Cr. brevis* | 3.00 ± 2.3Ba | 7.00 ± 4.3Aa | 30.7 ± 19.5Aa | 17.7 ± 10.9Aa | 42.3 ± 15.9Aa |
| Mean preference at RH[d] | 50.5 ± 9.3a | 14.5 ± 5.7b | 9.6 ± 5.3b | 10.3 ± 4.4b | 15.3 ± 5.5b |

[a]Means followed by the same lowercase letters within a row or means followed by the same capital letter within a column are not significantly different at the α = 0.05 level (Tukey honest significant difference test).
[b]Value for the combination (species × RH) of treatments are means of 6 observations of 50 termites per arena (25 termites for *N. jouteli*).
[c]Mean RH produced by water, 3 salts, and indicating Drierite are found in parentheses.
[d]Values for each main treatment effect (species, RH) are means of 30 and 24 observations, respectively.

**Table 3.** Effects of water source and species on worker survival (%) of 4 species of termite (*Coptotermes formosanus, Neotermes jouteli, Cryptotermes brevis,* and *Cryptotermes cavifrons*) from 1 to 4 wk (mean ± standard error of the mean [SEM]).

| | Water source[abc] | | | | | |
|---|---|---|---|---|---|---|
| | Wet wood | Dry wood | Wet soil | Wood + water | Wood + RH | |
| Species | (91.0 ± 0.22%) | (49.6 ± 0.61%) | (92.6 ± 0.22%) | (91.1 ± 0.22%) | (94.2 ± 0.18%) | Mean species survival[d] |
| Wk 1 | | | | | | |
| *C. formosanus* | 93.3 ± 6.7Aa | 0.0 ± 0.0Ab | 100 ± 0.0Aa | 100 ± 0.0Aa | 93.3 ± 3.3Aa | 77.3 ± 10.4A |
| *N. jouteli* | 96.7 ± 3.3Aa | 90.0 ± 10.0Ba | 96.7 ± 3.3Aa | 93.3 ± 3.3Aa | 100 ± 0.0Aa | 95.3 ± 2.2B |
| *Cr. cavifrons* | 86.7 ± 8.8Aa | 90.0 ± 10.0Ba | 93.3 ± 6.7Aa | 86.7 ± 13.3Aa | 76.7 ± 3.3Aa | 86.7 ± 3.7AB |
| *Cr. brevis* | 63.3 ± 21.9Aa | 86.7 ± 8.8Ba | 73.3 ± 13.3Aa | 80.0 ± 10.0Aa | 100 ± 0.0Aa | 80.7 ± 5.9AB |
| Mean survival with source[d] | 85.0 ± 6.6ab | 66.7 ± 12.1b | 90.8 ± 4.5a | 90.0 ± 4.3a | 92.5 ± 3.0a | |
| Wk 2 | | | | | | |
| *C. formosanus* | 90.0 ± 5.8Aa | 0.0 ± 0.0Ab | 96.7 ± 3.3Aa | 63.3 ± 31.8Aa | 90.0 ± 10.0Aa | 68.0 ± 11.2A |
| *N. jouteli* | 96.7 ± 3.3Aa | 90.0 ± 10.0Ba | 96.7 ± 3.3Aa | 96.7 ± 3.3Aa | 96.7 ± 3.3Aa | 95.3 ± 2.2B |
| *Cr. cavifrons* | 83.3 ± 6.7Aa | 90.0 ± 5.8Ba | 80.0 ± 11.5Aa | 100 ± 0.0Aa | 86.7 ± 3.3Aa | 88.0 ± 3.1AB |
| *Cr. brevis* | 26.7 ± 21.9Aa | 73.3 ± 21.9Ba | 56.7 ± 29.6Aa | 80.0 ± 11.5Aa | 80.0 ± 10.0Aa | 63.3 ± 9.4A |
| Mean survival with source[d] | 74.2 ± 9.8a | 63.3 ± 12.4a | 82.5 ± 8.4a | 85.0 ± 8.5a | 88.3 ± 3.7a | |
| Wk 3 | | | | | | |
| *C. formosanus* | 90.0 ± 5.8Aa | 0.0 ± 0.0Ab | 96.7 ± 3.3Aa | 90.0 ± 10.0Aa | 90.0 ± 5.8Aa | 73.3 ± 10.1AB |
| *N. jouteli* | 90.0 ± 10.0Aa | 83.3 ± 12.0Ba | 96.7 ± 3.3Aa | 86.7 ± 8.8Aa | 100 ± 0.0Aa | 91.3 ± 3.5A |
| *Cr. cavifrons* | 83.3 ± 8.8Aa | 96.7 ± 3.3Ba | 86.7 ± 6.7Aa | 93.3 ± 3.3Aa | 90.0 ± 0.0Aa | 90.0 ± 2.4A |
| *Cr. brevis* | 26.7 ± 26.7Aa | 80.0 ± 11.5Ba | 50.0 ± 26.5Aa | 60.0 ± 30.6Aa | 36.7 ± 12.0Aa | 50.7 ± 10.0B |
| Mean survival with source[d] | 72.5 ± 10.3a | 65.0 ± 12.0a | 82.5 ± 8.3a | 82.5 ± 8.2a | 79.2 ± 8.0a | |
| Wk 4 | | | | | | |
| *C. formosanus* | 100 ± 0.0Aa | 0.0 ± 0.0Ab | 96.7 ± 3.3Aa | 33.3 ± 33.3Aab | 96.7 ± 3.3ABa | 65.3 ± 12.4AC |
| *N. jouteli* | 86.7 ± 8.8ABa | 90.0 ± 0.0Ba | 93.3 ± 3.3Aa | 96.7 ± 3.3Aa | 83.3 ± 6.7ABa | 90.0 ± 2.4AB |
| *Cr. cavifrons* | 86.7 ± 8.8ABa | 100 ± 0.0Ba | 90.0 ± 10.0Aa | 73.3 ± 14.5Aa | 100 ± 0.0Aa | 90.0 ± 4.3B |
| *Cr. brevis* | 26.7 ± 14.5Ba | 83.3 ± 8.8Ba | 56.7 ± 3.3Aa | 36.7 ± 31.8Aa | 26.7 ± 14.5Ba | 46.0 ± 8.8C |
| Mean survival with source[d] | 75.0 ± 9.5a | 68.3 ± 12.2a | 84.2 ± 5.4a | 60.0 ± 13.0a | 76.7 ± 9.6a | |

[a]Weekly mean RH ± SEM associated with each water source are found in parentheses.
[b]Means for each combination of treatment (species × water source) followed by the same lowercase letters within a row or means followed by the same capital letter within a column are not significantly different at the α = 0.05 level (Tukey honest significant difference test).
[c]Values for each combination (species × water source) of treatments are means of 3 observations.
[d]Values for each main treatment effect (species, water source) are means of 15 and 12 observations, respectively.

distribution of *Microcerotermes crassus* Snyder (Termitidae), *Macrotermes carbonarius* (Hagen) (Termitidae), *Macrotermes gilvus* (Hagen) (Termitidae), *C. gestroi, C. formosanus, Reticulitermes speratus* (Kolbe) (Rhinotermitidae), *R. flavipes*, *Reticulitermes tibialis* Banks in Banks and Snyder (Rhinotermitidae), and *Reticulitermes virginicus* (Banks) (Rhinotermitidae) also highlights the importance of adequate water availability for other species (Delaplane & La Fage 1989; Nakayama et al. 2004, 2005; Green et al. 2005; McManamy et al. 2008; Wong & Lee 2010; Hu et al. 2012). Many termites (including *C. formosanus* and *N. jouteli*) are more likely to be found, survive longer, and consume food resources at higher rates in environments in which water resources are more likely to persist, but some, such as *Cr. brevis*, are not.

As reported for Kalotermitidae and Termopsidae by Collins (1991), the dampwood termite, *N. jouteli*, lives within its food source and requires moist conditions. However, *N. jouteli* and *Cr. cavifrons* inhabit wood pieces that are more likely to be subject to RH changes. Given that their geographic ranges include areas with extended wet and dry seasons, it is beneficial for them to be able to tolerate a range of RH and water availabilities. In this study, *Cr. cavifrons* and *N. jouteli* were able to tolerate conditions in which water sources were lacking, as well as utilize water sources when they were present.

As was noted by Pence (1956) and Collins (1958), the *Cryptotermes* species in this study were also less active than the subterranean and dampwood species, and tended to aggregate with little movement unless disturbed. *Coptotermes formosanus* and *N. jouteli,* while more active, also tended to aggregate. This aggregative huddling was likely a behavioral mechanism to prevent desiccation from water loss through evaporation from the body by decreasing overall surface area of the group. This behavior, termed the "group effect" by Grasse and Chauvin (1944), was reported to increase termite survival for several species (Pence 1956; Sen-Sarma & Chatterjee 1966; Minnick et al. 1973; Abushama 1974; Ahmad et al. 1982; Malik & Sheikh 1990; Cabrera & Rust 1996).

Another group behavior involved in desiccation tolerance is the consumption of nestmates. Cannibalism, as described by Collins (1991), was not explicitly observed in this study, but the fact that there were individuals missing from the *Neotermes* recovery study suggests they were probably cannibalized. This behavior is an additional means of obtaining water and food resources under water-stressed conditions.

Whereas some termites require access to water sources, too much moisture can be detrimental to other species. While each week of exposure was not statistically compared to the other weeks, there was a decrease in average survival from week 1 to 4 for *Cr. brevis*. There was also a decrease in survival for *Cr. brevis* when exposed to environments with RH >90%, and indicated that avoiding prolonged contact with free water is important to survival in this species. Our results agree with previous works of Collins (1969), Minnick et al. (1973), Steward (1982, 1983), Rudolph et al. (1990), and Woodrow et al. (2000), in which they found evidence of water toxicity in drywood termite species. If individuals of *Cr. brevis* could avoid direct contact with a water source, such as on the wood block provided, they were generally better able to tolerate these less-than-favorable environments with extended exposure.

Results of this study highlight the importance of water to the survival of four termite species and the differences in their RH preference, desiccation and RH tolerance, and moisture exposure tolerance. Further studies are needed to examine their morphological and physiological characteristics such as cuticular structure, spiracular openings, and cuticular permeability that may contribute to these differences.

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## References Cited

Abushama FT. 1974. Water-relations of the termites *Macrotermes bellicosus* (Smeathman) and *Trinervitermes geminatus* (Wasmann). Zeitschrift fur Angewandte Entomologie 75: 124–134.

Ahmad M, Afzal M, Salihah Z. 1982. The effects of different relative humidities on survival and moisture loss of workers and soldiers of *Heterotermes indicola* (Wasmann) (Isoptera: Rhinotermitidae) under starvation conditions. Pakistan Journal of Zoology 14: 652–670.

Arab A, Costa-Leonardo AM. 2005. Effect of biotic and abiotic factors on the tunneling behavior of *Coptotermes gestroi* and *Heterotermes tenuis* (Isoptera: Rhinotermitidae). Behavioural Processes 70: 32–40.

Brammer AS, Scheffrahn RH. 2007. A drywood termite. *Cryptotermes cavifrons* Banks (Insecta: Isoptera: Kalotermitidae). University of Florida Institute of Food and Agricultural Services, Entomology & Nematology Department, http://entomology.ifas.ufl.edu/creatures/urban/termites/c_cavifrons.htm (last accessed 15 Apr 2017).

Cabrera BJ, Rust MK. 1996. Effect of temperature and relative humidity on aggregation and water loss in the Western drywood termite, *Incisitermes minor* (Hagen). Proceedings of the National Conference on Urban Entomology 1: 39–41.

Collins M. 1958. Studies on water relations in Florida termites. I. Survival time and rate of water loss during drying. Quarterly Journal of the Florida Academy of Sciences 21: 341–352.

Collins M. 1963. Studies on water relations in North American termites I. Eastern species of the genus *Reticulitermes* (Isoptera, Rhinotermitidae). Ecology 44: 600–604.

Collins M. 1966. Studies on water relations in North American termites II. Water loss and cuticular structures in eastern species of the Kalotermitidae (Isoptera). Ecology 47: 328–331.

Collins M. 1969. Water relations in termites, pp. 433–458 *In* Krishna K, Weesner FM [eds.], Biology of Termites, Vol. 1. Academic Press, New York.

Collins M. 1991. Physical factors affecting termite distribution. Sociobiology 19: 283–286.

Delaplane KS, La Fage JP. 1989. Preference for moist wood by the Formosan subterranean termite (Isoptera: Rhinotermitidae). Journal of Economic Entomology 82: 95–100.

Gallagher NT, Jones SC. 2010. Moisture augmentation of food items by *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). Sociobiology 55: 735–747.

Gautam BK, Henderson G. 2011. Relative humidity preferences and survival of starved Formosan subterranean termites (Isoptera: Rhinotermitidae) at various temperature and relative humidity conditions. Environmental Entomology 40: 1232–1238.

Gautam, BK, Henderson G. 2014. Water transport by *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Environmental Entomology 43: 1399–1405.

Grasse PP, Chauvin R. 1944. L'effect de group et la survie des neutres dans les societies d'Insectes. Revue Scientifique 82: 461–464.

Green JM, Scharf ME, Bennett GW. 2005. Impacts of soil moisture level on consumption and movement of three sympatric subterranean termites (Isoptera: Rhinotermitidae) in a laboratory assay. Journal of Economic Entomology 98: 933–937.

Grube S, Rudolph D. 1999a. The labial gland reservoirs (water sacs) in *Reticulitermes santonensis* (Isoptera: Rhinotermitidae): studies of the functional aspects during microclimatic moisture regulation and individual water balance. Sociobiology 33: 307–323.

Grube S, Rudolph D. 1999b. Water supply during building activities in the subterranean termite *Reticulitermes santonensis* De Feytaud (Isoptera, Rhinotermitidae). Insectes Sociaux 46: 192–193.

Hu J, Neoh K-B, Appel AG, Lee C-Y. 2012. Subterranean termite open-air foraging and tolerance to desiccation: comparative water relation of two sympatric *Macrotermes* spp. (Blattodea: Termitidae). Comparative Biochemistry and Physiology A: Physiology 161: 201–207.

Khan MA. 1980. Effect of relative humidity on survival of termites under starvation conditions. Zeitschrift fur Angewandte Entomologie 67: 133–178.

Lee KE, Wood TG. 1971. Termites and Soils. Academic Press, New York.

Malik SA, Sheikh KH. 1990. Effect of different relative humidities on survival and moisture loss of termite workers and soldiers. Pakistan Journal of Zoology 22: 159–165.

McManamy K, Koehler PG, Branscome DD, Pereira RM. 2008. Wood moisture content affects the survival of Eastern subterranean termites (Isoptera: Rhinotermitidae), under saturated relative humidity conditions. Sociobiology 52: 145–156.

Minnick DR, Kerr SH, Wilkinson RC. 1973. Humidity behavior of the drywood termite *Cryptotermes brevis*. Environmental Entomology 2: 597–601.

Nakayama T, Yoshimura T, Imamura Y. 2004. Recovery of Japanese subterranean termites, *Reticulitermes speratus* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae), from desiccation treatment. Sociobiology 43: 489–499.

Nakayama T, Yoshimura T, Imamura Y. 2005. Feeding activities of *Coptotermes formosanus* Shiraki and *Reticulitermes speratus* (Kolbe) as affected by moisture content of wood. Journal of Wood Science 51: 60–65.

Pence RJ. 1956. The tolerance of the drywood termite, *Kalotermes minor* Hagen, to desiccation. Journal of Economic Entomology 49: 553–554.

Rockland LB. 1960. Saturated salt solutions for static control of relative humidity between 5° and 40°C. Analytical Chemistry 32: 1375–1376.

Rudolph D, Glocke B, Rathenow S. 1990. On the role of different humidity parameters for the survival, distribution and ecology of various termite species. Sociobiology 17: 129–140.

Rust MK, Reierson DA, Scheffrahn RH. 1979. Comparative habits, utilization and xeric adaptations of the Southwestern drywood termites, *Incisitermes fruticavus* Rust and *Incisitermes minor* (Hagen) (Isoptera: Kalotermitidae). Sociobiology 4: 239–255.

SAS. 2015. Using JMP Pro 11. SAS Institute Inc., Cary, North Carolina.

Scheffrahn RH, Su N-Y. 2007. West Indian drywood termite. *Cryptotermes brevis* (Walker) (Insecta: Isoptera: Kalotermitidae). University of Florida Institute of Food and Agricultural Services, Entomology & Nematology Department, http://entomology.ifas.ufl.edu/creatures/urban/termites/west_indian_drywood_termite.htm (last accessed 15 Apr 2017).

Sen-Sarma PK, Chatterjee PN. 1966. Humidity behavior of termites. I. Effect of relative humidity on the longevity of workers of *Microcerotermes beesoni* Snyder (Insecta: Isoptera: Termitidae) under starvation condition. Forest Bulletin no. 23. Forest Research Institute, Dehra Dun (Entomology), India.

Sponsler RC, Appel AG. 1990. Aspects of the water relations of the Formosan and Eastern subterranean termites (Isoptera: Rhinotermitidae). Environmental Entomology 19: 15–20.

Steward RC. 1982. Comparison of the behavioral and physiological responses to humidity of five species of dry-wood termites, *Cryptotermes* species. Physiological Entomology 7: 71–82.

Steward RC. 1983. The effects of humidity, temperature and acclimation on the feeding, water balance and reproduction of dry-wood termites (*Cryptotermes*). Entomologia Experimentalis et Applicata 33: 135–144.

Strickland M. 1950. Differences in toleration of drying between species of termites (*Reticulitermes*). Ecology 31: 373–385.

Su N-Y, Puche H. 2003. Tunneling activity of subterranean termites (Isoptera: Rhinotermitidae) in sand with moisture gradients. Journal of Economic Entomology 96: 88–93.

Su N-Y, Scheffrahn RH. 1986. A method to access, trap, and monitor field populations of the Formosan termite (Isoptera: Rhinotermitidae) in the urban environment. Sociobiology 12: 299–304.

Winston PW, Bates DH. 1960. Saturated solutions for the control of humidity in biological research. Ecology 41: 232–237.

Wong N, Lee C-Y. 2010. Influence of different substrate moistures on wood consumption and movement patterns of *Microcerotermes crassus* and *Coptotermes gestroi* (Blattodea: Termitidae, Rhinotermitidae). Journal of Economic Entomology 103: 437–442.

Woodrow RJ, Grace JK, Nelson LJ, Haverty MI. 2000. Modification of cuticular hydrocarbons of *Cryptotermes brevis* (Isoptera: Kalotermitidae) in response to temperature and relative humidity. Environmental Entomology 29: 1100–1107.