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Research

Erythritol Ingestion Causes Concentration-Dependent Mortality in Eastern Subterranean Termites (Blattodea: Rhinotermitidae)

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Abstract

Damage from termite infestations is economically significant and control can be costly when requiring the widespread use of conventional insecticides. Erythritol, a polyalcohol sweetener that is safe for human consumption, causes increased mortality when ingested by some insects, indicating potential as a safe alternative insecticide. Here, we investigated the applicability of erythritol as a novel toxicant method of termite control. Eastern subterranean termites, *Reticulitermes flavipes* Kollar (Blattodea: Rhinotermitidae), were fed paper foods treated with increasing concentrations of erythritol and were assessed for mortality and bait consumption. Termite survival to 8 d (the duration of the experiment) significantly decreased as erythritol treatment concentration increased, indicating that the lethal effects of erythritol were concentration-dependent. Termites consumed erythritol-treated paper at all concentrations and did not display avoidance in choice assays, suggesting that erythritol may be practical for use as an ingestible bait. These results provide a basis for further development of erythritol as a safe alternative method of termite control.

Key words: erythritol, alternative insecticide, termite control

Erythritol is a polyalcohol, low-calorie sweetener that is safe for ingestion by humans and other mammals (Bernt et al. 1996, Storey et al. 2007), but acts as an effective and palatable insecticide to house flies, fire ants, and both adult and larval fruit flies and mosquitos (Baudier et al. 2014, O'Donnell et al. 2016, Choi et al. 2017, Fisher et al. 2017, Zhang et al. 2017, Gilkey et al. 2018, O'Donnell et al. 2018). The effects of erythritol on the eastern subterranean termite, a major economic pest, have not yet been assessed. Infestations by subterranean termites can pose significant damage to residential, commercial, and agricultural structures (Constantino 2002), making the development of new, alternative methods of control desirable. In addition, understanding erythritol's impact on different insect taxa may help in understanding its mechanism of lethality.

In this study, we tested the effects of erythritol ingestion in eastern subterranean termites, *Reticulitermes flavipes* Kollar (Blattodea: Rhinotermitidae). We measured termite worker longevity following erythritol consumption, documented consumption of erythritol-treated papers at several concentrations, and tested for feeding preference on paper with and without erythritol. Termite worker longevity to 8 d (the duration of the study period) was compared across multiple erythritol concentrations (0–1.25 M, in 0.25 M increments). To confirm the consumption of erythritol by workers, we used filter papers treated with erythritol and blue dye, which was visible in the termite hindgut following consumption. Finally, we performed a choice experiment to test if termites preferred or avoided erythritol-treated foods when given access to control foods.

Methods

Termite Collection

Termites used in the survival and choice experiments were collected from three field colonies in Scotland Run Park (39.66°N, 75.05°W) in Clayton, NJ between April and May 2019. After collection, colonies were maintained in plastic containers with soil and wood from the collection site as a substrate in laboratory conditions (20.8 ± 0.9°C, 49 ± 7% RH). Termites used in the consumption experiment were collected from a single field colony at Cobb's Creek Park (39.94°N, 75.24°W) in Philadelphia, PA during September of 2018. Workers were removed from the log and housed within 24 h

of collection in 9 cm diameter petri dishes containing damp paper towel as a food source. Dishes were placed in an incubator at 26°C (relative humidity varied between 40 and 60% across trials, but was consistent among all treatments within each trial). Each petri dish contained 10 workers. Termites used in all experiments measured 3–4 mm in length.

Paper Food Preparation

For the survival experiment, unbleached, brown paper towels (12 cm × 24 cm, cat no. 01801, Kimberly-Clark Corporation, Neenah, WI), were completely submerged for 15 s in solution of distilled water, erythritol (100% purity, NOW foods, Bloomingdale, IL) of the below-specified concentrations, and 0.05% Brilliant Blue R-250 dye (cat. no 27816, Sigma–Aldrich, St. Louis, MO). The erythritol concentrations used were: 0 M (control), 0.25 M, 0.5 M, 0.75 M, 1.0 M, and 1.25 M. The treated paper towels were removed from solution and allowed to dry horizontally on racks before being cut into squares with an area of 144 cm^2. Papers were thereafter stored dry at room temperature in sealed containers.

For the consumption trial and choice assays, white filter papers were used instead of brown paper towels, which allowed for more obvious detection of blue dye in the gut during consumption trials and also retained moisture better during the choice assay. Filter papers (15 cm diameter, filter paper 413, cat no. 28310-128, VWR, Radnor, PA) were submerged in solution of distilled water, erythritol (100% purity, NOW foods, Bloomingdale, IL) in the below-specified concentrations, and 0.05% Brilliant Blue R-250 dye (cat. no 27816, Sigma–Aldrich, St. Louis, MO) for 15 s. The erythritol concentrations used were as follows: 0 M (control), 0.25 M, 0.5 M, 0.75 M, 1.0 M, and 1.5 M. The treated filter papers were allowed to dry horizontally on racks in an oven at 60°C, before being cut to a final area of 44.2 cm^2 (circles cut into quarters), and thereafter stored dry at room temperature in sealed containers. For choice trials, treated filter papers were cut into 2 cm diameter disks.

Concentration-Dependent Effects of Erythritol on Termite Longevity

Prior to the beginning of the experiment, termites were allowed to acclimate for 3 d to the petri dishes, in order to control for any death due to injury incurred during movement to the petri dishes; this was called the pretrial period. At the beginning of the pretrial period, termites used in the survival experiment were transferred from sections of natural nest kept in laboratory rearing boxes to 9 cm diameter plastic petri dishes lined with brown, unbleached paper towel (12 cm × 24 cm) not treated with erythritol. The paper towel was rehydrated with 1 ml of distilled water. Each dish contained 10 workers. After the third (final) day of the pretrial period, dishes were checked for dead termites, assumed to be dead due to injury, and dead termites were replaced with live individuals from a petri dish of extra termites kept in similar conditions.

Following the pretrial period, the experiment was set up: pretrial paper towels were removed and replaced with treated paper towels of the correct erythritol treatment concentration; these were rehydrated with 750 µl of distilled water. Six treatment groups (0 M, 0.25 M, 0.5 M, 0.75 M, 1.0 M, 1.25 M erythritol) were used per colony (n = 3 colonies), with three dishes per treatment, each containing 10 termite workers (n = 30 workers/treatment/colony, n = 540 total workers). Termite mortality was recorded every 24 h for 8 d.

Assessing Erythritol Consumption Using Blue Dye

To confirm that termites consumed erythritol-treated filter paper, papers were stained with blue dye, which was visible through the exoskeleton of the worker's abdomens after consumption. For this experiment, a pretrial period of 1 d was used to allow termites to acclimate to experiment conditions. Termites that had previously been placed in petri dishes directly after field collection were checked for survival at the end of the 24-h pretrial period. Dead individuals were removed and replaced with live individuals. Dishes were then assigned to treatment groups and paper towels were replaced with blue-stained, erythritol-treated filter papers, which were rehydrated with 750 µl distilled water. White filter papers were used in this experiment instead of unbleached paper towels because the brown color of the unbleached towels interfered with our ability to assess the presence of blue dye in the gut. Six treatment groups (0 M, 0.25 M, 0.5 M, 0.75 M, 1.0 M, 1.5 M erythritol), with three dishes per treatment, each containing 10 termite workers (n = 30 workers/treatment, n = 180 total workers) were assessed for the presence of blue dye, visible through the exoskeleton, in the gut of dead individuals every 24 h for 8 d. Treated paper towels were replaced, and new paper towels rehydrated with water, every 4 d. Replacement was necessary to maintain adequately sanitary conditions inside the petri dishes.

Choice Test

Choice arenas were constructed from 9 cm diameter plastic petri dishes containing two, 2 cm diameter filter paper disks placed 2 cm apart in the center of the arena, rehydrated with 50 µl distilled water each (methods adapted from Bläske and Hertel 2009). During each trial, termites were exposed to either paired control-control disks (two, 0 M erythritol disks), treatment-treatment disks (two, 1.25 M erythritol disks), or control-treatment disks (one each 0 M and 1.25 M erythritol disks). Fifty termites were placed in each choice arena, and choice arenas were placed in a closed cardboard box to minimize light disturbance. Three replicates, each using a different colony (n = 50 workers/colony/treatment for a total of 150 termites per treatment), were performed for each choice combination (total n = 450). Termite attendance at either filter paper disk was recorded by photographing the dishes. Recording began 5 min after termites were placed in dishes with disks, and every 5 min thereafter for 1 h, totaling 12 observations. Termites not attending either disk were not counted. No termites died during the choice trials.

Statistical Analyses

Analyses were performed using SPSS v. 24 (IBM corp. 2016) and Sigmaplot v.12.5 (Systat Software 2013) software. Differences in survival distributions across concentrations for all colonies, within the colonies, and across colonies were tested using pairwise log-rank Mantel Cox tests in SPSS, with subjects living to the end of the trial or lost to reasons other than death (e.g., escaped or injured) included in the analysis as right-censored values. Mean percent mortality was calculated for each concentration across colonies at 72 and 96 h and a three parameter, best-fit sigmoid curve was fitted to the data in Sigmaplot to assess LC_{50} at these time points.

Relative forager preference at each time point was determined (as in El-Keredy et al. 2012) as:

$$PREF(ert) = \frac{\#\ termites\ on\ erythritol\ paper - \#\ termites\ on\ control\ paper}{total\ \#\ of\ termites\ foraging\ at\ that\ time\ point}$$

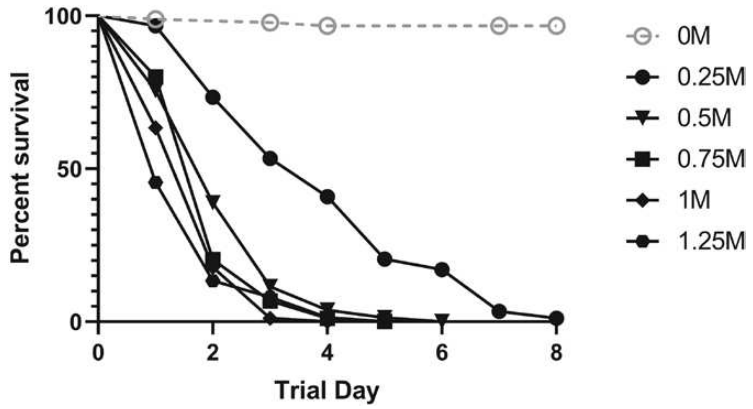

Fig. 1. Erythritol ingestion causes concentration-dependent mortality in *R. flavipes* workers. Survival plot showing percent survival of worker *R. flavipes* ($n = 90$ workers/concentration) over time. Individual lines represent treatment groups receiving filter paper treated with increasing concentrations of erythritol (0–1.25 M). All treatments are significantly different from 0 M.

The relative preference values from the 12 time points were then averaged, to get an overall relative forager preference over the course of the trial. This method constrains the preference values between 1 and −1, with positive values indicating a preference for erythritol and negative values indicative of avoidance. Differences in relative forager preference between 1.25 M/0 M, 0 M/0 M, and 1.25 M/1.25 M trials were assessed using a Kruskal–Wallis test. Differences between the relative preference within each trial and a random chance relative preference (i.e., 50% of foraging termites on each filter paper disk on average over the trial) were tested using one sample *t*-tests (with a value of 0 relative preference in the one sample *t*-test representing random chance; El-Keredy et al. 2012).

Results

Concentration-Dependent Mortality

Longevity of *R. flavipes* workers to 8 d differed significantly between 0 M control and all erythritol concentration treatments (Fig. 1: Mantel-Cox, 0.25M: $X^2 = 179.93$, $P < 0.001$; 0.5 M: $X^2 = 184.64$, $P < 0.001$; 0.75 M: $X^2 = 189.60$, $P < 0.001$; 1 M: $X^2 = 188.34$, $P < 0.001$; 1.25 M: $X^2 = 189.90$, $P < 0.001$). Longevity was also concentration-dependent (Fig. 1). Concentration dependence lessened at higher concentrations: there was only a moderately significant difference between 0.75 M and 1.0 M treatments ($X^2 = 4.86$, $P = 0.027$), and no significant difference between 0.5 M and 0.75 M ($X^2 = 2.84$, $P = 0.09$) or between 1.0 M and 1.25 M treatments ($X^2 = 1.04$, $P = 0.31$). The magnitude of the decrease in mean termite longevity differed between subsequent increases in treatment concentration (Fig. 2). The decrease in mean longevity was greatest as concentration increased from 0 M to 0.25 M (Fig. 2; reduction in mean longevity of 3.77 d) and 0.25 M to 0.5 M (reduction in mean longevity of 1.74 d). Reduction in mean longevity was smaller between higher subsequent concentrations (Fig. 2; 0.5–0.75 M: reduction of 0.23 d; 0.75–1.0 M: reduction of 0.26 d; 1.0–1.25 M: reduction of 0.14 d).

LC_{50} Estimates

The best-fit sigmoidal curve for 24 h LC_{50} data was:

$$\text{Percent (mortality at 24 h)} = 109.26/\left(1+e^{(-([\text{Erythritol}]-0.1.26)/0.40)}\right)$$

This curve was a significantly good fit to the data ($R^2 = 0.92$, $P = 0.0207$) and using the equation we estimated the LC_{50} at 24 h to be 1.19 M erythritol.

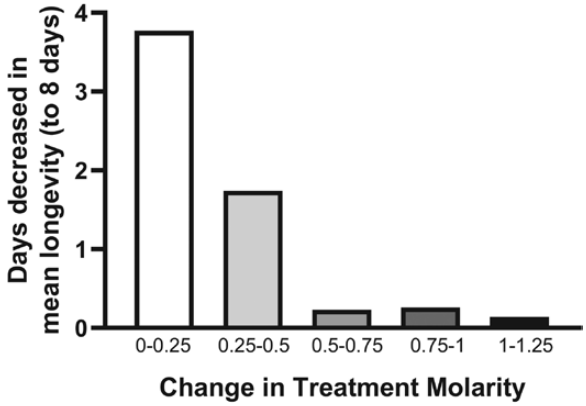

Fig. 2. Erythritol ingestion causes larger changes in longevity at lower concentrations. Decrease in mean longevity to 8 d between consecutive increases (0–1.25 M) in treatment molarity.

The best-fit sigmoidal curve for 48 h LC_{50} data was:

$$\text{Percent (mortality at 48 h)} = 84.56/\left(1+e^{(-([\text{Erythritol}]-0.37)/0.13)}\right)$$

This curve was a significantly good fit to the data (Fig. 3: $R^2 = 0.996$, $P = 0.0003$) and using the equation we estimated the LC_{50} at 48 h to be 0.42 M erythritol.

Intercolony Variation in Erythritol Effects on Longevity

Colonies differed in their response to erythritol (Fig. 4: Mantel-Cox, 0M: $X^2 = 0$, $P = 1.00$; 0.25 M: $X^2 = 42.79$, $P < 0.001$; 0.5 M: $X^2 = 17.55$, $P < 0.001$; 0.75 M: $X^2 = 9.05$, $P = 0.011$; 1 M: $X^2 = 22.89$, $P < 0.001$; 1.25 M: $X^2 = 14.80$, $P = 0.001$). This difference was exhibited as early as day 1, indicating erythritol was more immediately toxic to some colonies (Mantel-Cox, 0 M: $X^2 = 2.00$, $P = 0.37$; 0.25 M: $X^2 = 6.14$, $P = 0.046$; 0.5 M: $X^2 = 12.97$, $P = 0.002$; 0.75 M: $X^2 = 11.54$, $P = 0.003$; 1 M: $X^2 = 26.40$, $P < 0.001$; 1.25 M: $X^2 = 29.33$, $P < 0.001$).

Confirmation of Consumption of Treated Filter Papers

Of the treatment termites that died in the consumption test, 81% had blue dye visible in their guts through the exoskeleton, confirming that they had ingested erythritol-treated filter papers.

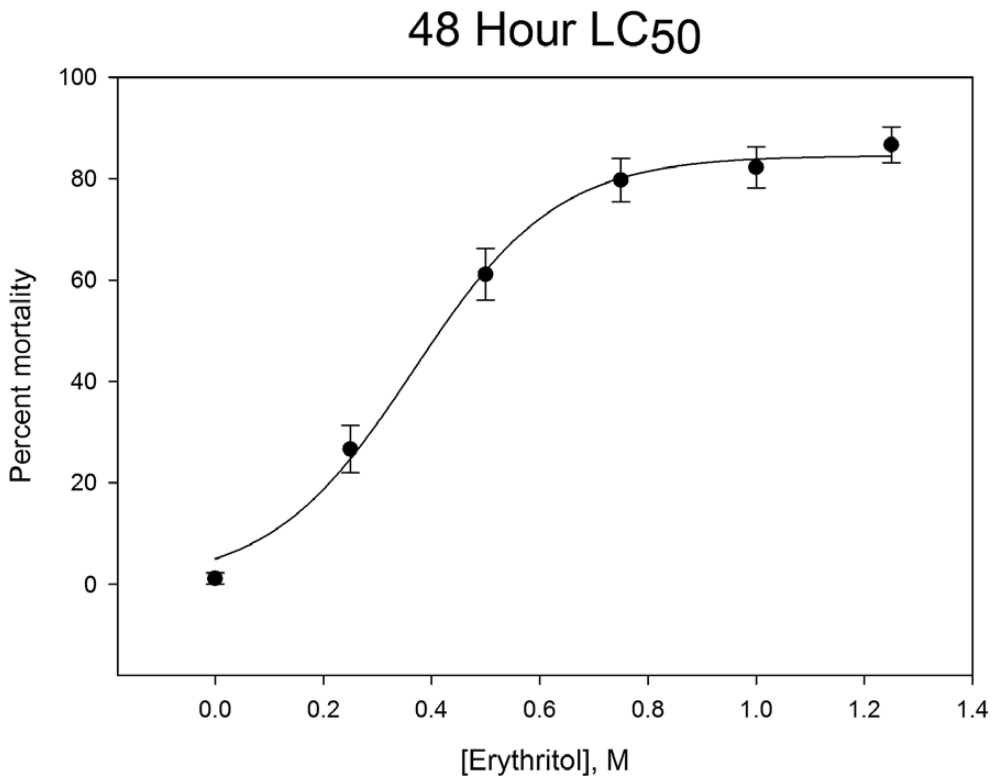

Fig. 3. The LC_{50} of erythritol at 48 h is 0.42 M for *R. flavipes* workers. Percent mortality at 48 h plotted against concentration of erythritol used for treating filter papers. The three-parameter, best-fit sigmoidal curve is shown and the function was used to calculate LC_{50} at 48 h (0.42 M). Error bars represent one standard deviation.

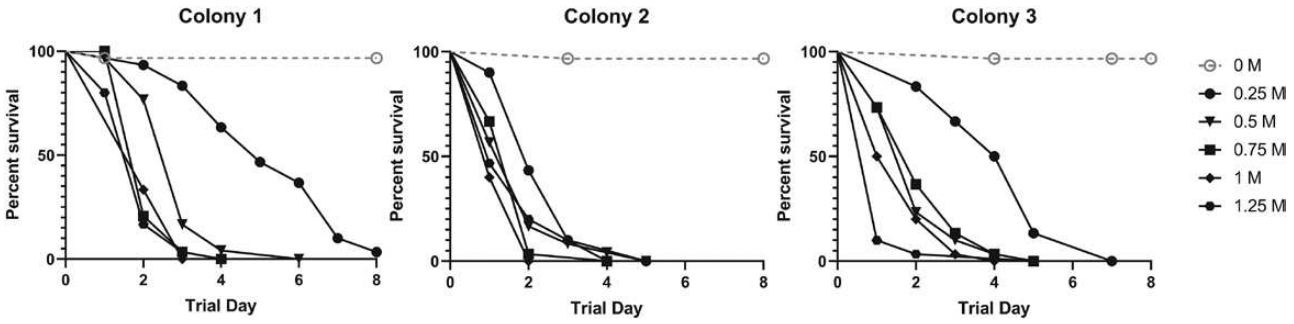

Fig. 4. Colonies vary in worker susceptibility to erythritol toxicity. Survival plots showing percent survival of worker *R. flavipes* over time from three different colonies (n = 30 workers/treatment/colony). Individual lines represent treatment groups receiving filter papers treated with increasing concentrations of erythritol (0–1.25 M). Colonies differed significantly at all concentrations.

No Avoidance of Erythritol at 1.25 M

Termites did not differ in their relative preference for 1.25 M erythritol versus 0 M erythritol-treated filter paper disks when compared with preferences in either the 0 M/0 M or 1.25 M/1.25 M tests (Kruskal–Wallis, KW = 0.08, P = 0.99). None of the three tests differed in their relative preference from random chance (one sample t-test, 0 M/1.25 M, t = 0.42, P = 0.72; 0 M/0 M, t = 0.33, P = 0.77; 1.25 M/1.25 M, t = 0.36, P = 0.75).

Discussion

Erythritol is toxic to multiple insect taxa when ingested, including fruit flies, mosquitoes, and ants (Baudier et al. 2014, Zheng et al. 2016, Zhang et al. 2017, Gilkey et al. 2018). In this experiment, we found that erythritol consumption also reduced *R. flavipes* worker longevity in a concentration-dependent manner, with significant effects on longevity starting at 0.25 M erythritol. While longevity decreased with increasing concentration, the magnitude of the mean reduction in longevity was not consistent between consecutive increases in concentration; the reduction in mean longevity was greater between increases at lower concentrations (e.g., 0–0.25 M; 0.25–0.5 M), compared to the reduction in mean longevity at higher concentrations (e.g., 0.5–0.75 M and above). These results indicate that while survival and longevity are indeed concentration dependent, and mean longevity is lowest at the highest treatment concentrations, increases in concentration above 0.5 M do not yield proportionally greater increases in efficacy.

Our longevity experiment also found significant intercolony differences in susceptibility to the effects of erythritol. Susceptibility to other insecticides can vary substantially between termite colonies (Osbrink et al. 2001). The variation in susceptibility to erythritol may indicate a

genetic component to erythritol's mechanism of lethality, or it could indicate colony differences in environmental experience prior to testing. Despite these intercolony differences, workers from all tested colonies were susceptible to relatively low concentrations of erythritol, and intercolony variation did not substantially decrease erythritol efficacy.

The mechanism of erythritol's lethality may be linked to osmotic balance. In mosquitoes exposed to erythritol, mortality is partially rescued with access to extra water (Gilkey et al. 2018), and erythritol changes osmotic pressure in the fly hemolymph (Tang 1999, Choi et al. 2017). Further, polyol ingestion induces hyper-regurgitation in flies, which may be a response to osmotic shock (Díaz-Fleischer et al. 2019). The rate of termite mortality found in our study was high compared to similar experiments conducted by Baudier et al. (2014) using fruit flies. In Baudier's work, 50% mortality was achieved in fruit flies after 20 d of exposure to 0.5 M erythritol food. In our study, termites reached 50% mortality within 2 d of exposure to 0.5 M erythritol filter papers. Considering termite intolerance of desiccation (Woon et al. 2018), this comparatively increased rate of mortality supports the notion that water balance disruption could be part of the mechanism causing increased mortality in termites.

We confirmed that erythritol was consumed by termites at all treatment concentrations, as indicated by the presence of blue dye visible through the exoskeleton of 81% of dead termites. The mortality observed in termites with no blue visible in the gut may be attributed to injury or stress during the removal of termites from the nest and transfer into petri dishes.

Though consumption indicated that termites do not reject erythritol, a choice assay was necessary to determine whether termites would avoid erythritol-treated food if offered an alternative (i.e., untreated paper). We found no difference in termite attendance of 1.25 M erythritol or control disks when termites were given a choice. While the choice assay did not measure consumption, absence of individuals at a food source can serve as an indication of avoidance (Bläske and Hertel 2009). Thus, the equal attendance of termites at control and erythritol-treated filter paper disks suggests they do not avoid erythritol, even at very high concentrations. However, it is unknown whether termites are able to detect erythritol. Random attendance at filter paper disks may be due to lack of preference for control foods compared to erythritol-treated foods; this could indicate that termites are unable to sense erythritol. Fire ants cannot detect erythritol in foods (Vander Meer et al. 1995). Feeding choice assays performed on *R. flavipes* (formerly *R. santonensis*) found that erythritol did not stimulate feeding behavior (Rienhard and Kaib 2001). However, thin-layer chromatography analysis showed that erythritol occupies the same biologically active, phagostimulatory zone as termite labial gland secretions, indicating that erythritol and the secretions likely have similar physicochemical properties (Rienhard and Kaib 2001), and thus may be detected by termites. Even if termites can detect erythritol, our choice assay suggests that termites do not display preference or avoidance of the compound in the presence of alternative food sources.

Our experiments demonstrated that erythritol is effective at reducing termite longevity in a concentration-dependent manner, and that termites do not display avoidance to erythritol, supporting its potential to be used as an ingestible insecticide. Insecticides for social insects that rely on ingestion by workers must be nonrepellant and slow-acting, in order to be effectively transferred through the colony (Su et al. 1982). Further trials are needed to determine the appropriate application concentrations for *R. flavipes*. Additionally, we did not assess the potential for erythritol to be spread through a colony. Previous work has found that ants transfer erythritol between individuals and castes (Zhang et al. 2017), but the efficacy with which erythritol is transferred through a termite colony via trophallaxis has not yet been assessed.

References Cited

Baudier, K. M., S. D. Kaschock-Marenda, N. Patel, K. L. Diangelus, S. O'Donnell, and D. R. Marenda. 2014. Erythritol, a non-nutritive sugar alcohol sweetener and the main component of Truvia®, is a palatable ingested insecticide. PLoS One. 9: 1–7.

Bernt, W. O., J. F. Borzelleca, G. Flamm, and I. C. Munro. 1996. Erythritol: a review of biological and toxicological studies. Regul. Toxicol. Pharmacol. 24: S191–S197.

Bläske, V.-U., and H. Hertel. 2009. Repellent and toxic effects of plant extracts on subterranean termites (Isoptera: Rhinotermitidae). J. Econ. Entomol. 94: 1200–1208.

Choi, M. Y., S. B. Tang, S. J. Ahn, K. G. Amarasekare, P. Shearer, and J. C. Lee. 2017. Effect of non-nutritive sugars to decrease the survivorship of spotted wing drosophila, *Drosophila suzukii*. J. Insect Physiol. 99: 86–94.

Constantino, R. 2002. The pest termites of South America taxonomy, distribution and status. J. Appl. Entomol. 126: 355–365.

Díaz-Fleischer, F., J. Arredondo, R. Lasa, C. Bonilla, D. Debernardi, D. Pérez-Staples, and T. Williams. 2019. Sickly sweet: insecticidal polyols induce lethal regurgitation in Dipteran pests. Insects. 10: 53.

El-Keredy, A., M. Schleyer, C. König, A. Ekim, and B. Gerber. 2012. Behavioural analyses of quinine processing in choice, feeding and learning of larval *Drosophila*. Plos One. 7: e40525.

Fisher, M. L., F. E. Fowler, S. S. Denning, and D. W. Watson. 2017. Survival of the house fly (Diptera: Muscidae) on Truvia and other sweeteners. J. Med. Entomol. 54: 999–1005.

Gilkey, P. L., D. T. Bolshakov, J. G. Kowala, L. A. Taylor, S. O'Donnell, D. R. Marenda, and L. K. Sirot. 2018. Lethal effects of erythritol on the mosquito *Aedes aegypti* Linnaeus (Diptera: Culicidae). J. Appl. Entomol. 142: 873–881.

IBM Corp. 2016. IBM SPSS statistics for windows, version 24.0. IBM Corp, Armonk, NY.

O'Donnell, S., K. Baudier, and D. R. Marenda. 2016. Non-nutritive polyol sweeteners differ in insecticidal activity when ingested by adult *Drosophila melanogaster* (Diptera: Drosophilidae). J. Insect Sci. 16: 2016–2018.

O'Donnell, S., K. Baudier, K. Fiocca, and D. R. Marenda. 2018. Erythritol ingestion impairs adult reproduction and causes larval mortality in *Drosophila melanogaster* fruit flies (Diptera: Drosophilidae). J. Appl. Entomol. 142: 37–42.

Osbrink, W. L. A., A. R. Lax, and R. J. Brenner. 2001. Insecticide susceptibility in *Coptotermes formosanus* and *Reticulitermes virginicus* (Isoptera : Rhinotermitidae) (Isoptera : Rhinotermitidae). J. Econ. Entomol. 94: 1217–1228.

Rienhard, J., and M. Kaib. 2001. Thin-layer chromatography assessing feeding stimulation by labial gland secretion compared to synthetic chemicals in the subterranean termite *Reticulitermes santonensis*. J. Chem. Ecol. 27: 175–187.

Storey, D., A. Lee, F. Bornet, and F. Brouns. 2007. Gastrointestinal tolerance of erythritol and xylitol ingested in a liquid. Eur. J. Clin. Nutr. 61: 349–354.

Su, N.-Y., M. Tamashiro, J. R. Yates, and M. I. Haverty. 1982. Effect of behavior on the evaluation of insecticides for ptevention of or remedial control of the Formosan subterranean termite. J. Econ. Entomol. 75: 188–193.

Systat Software. 2013. Sigmaplot. Version 12.5. Systat Software, San Jose, CA.

Tang, S. B. 1999. Physiological effects of non-nutritive sugars on the survivorship and fecundity of *Drosophila suzukii* (Diptera: Drosophilidae). M.S. Diss. Oregon State Univ., Corvallis, OR.

Vander Meer, R. K., C. S. Lofgren, and J. A. Seawright. 1995. Specificity of the red imported fire ant (Hymenoptera: Formicidae) phagostimulant response to carbohydrates. Fl. Entomol. 78: 144–154.

Woon, J. S., M. Boyle, R. M. Ewers, A. Chung, and P. Eggleton. 2018. Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests. Insectes Soc. 66: 57–64.

Zhang, X., S. Chen, Z. Li, and Y. Xu. 2017. Effect of sweeteners on the survival of *Solenopsis invicta* (Hymenoptera: Formicidae). J. Econ. Entomol. 110: 593–597.

Zheng, C., L. Zeng, and Y. Xu. 2016. Effect of sweeteners on the survival and behaviour of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae). Pest Manag. Sci. 72: 990–996.