NOT SINGING IN THE RAIN: *NASUTITERMES CORNIGER* RESPONSE TO TRAIL DISTURBANCE IN THE PRESENCE OF WATER

R. QUINN THOMAS, HEATHER E. LAPIN AND PETER N. CHALMERS

Abstract: Termites in tropical wet regions, but not elsewhere, build covered trails to food sources. It is not known why termites build these trails. We tested the hypothesis that covered trails have evolved for rain protection by comparing the efficacy of trail repairs with and without simulated rainfall and found termite rebuilding ability to be significantly hampered in wet conditions. Contrary to the hypothesis, trail repair required at least 77% longer in the presence of water. We propose three alternate explanation for the trails existence: (1) to provide a microclimate for the termites, (2) to protect against predation, and (3) to protect pheromone-based communication systems within the colony.

Key words: arboreal nests, communication, pheromones, termite

INTRODUCTION

Termites occur worldwide, but tropical termites build nests using carton, fecal glue that the workers secrete (Borrow and White 1970). Additionally, it appears that only termites in rainforests and seasonally wet forests build carton trails to food sources, but the trail's function is unknown (Lubin 1983 and Holmes, pers. comm.) Rainfall is an important abiotic factor in the rainforests and dry deciduous forests where trails are found. Therefore, water may be a threat to the colony and affect the behavior of termites. We hypothesized that trails are built to protect the termites from the threat of water, and predicted that termites will rebuild a trail breach quicker under wet conditions. To test this prediction we examined how the rebuilding of a trail breach by *Nasutitermes corniger* differed under wet and dry conditions.

METHODS

We measured the breach rebuilding ability of 19 colonies of *N. corniger* in Palo Verde National Park, Costa Rica on 14 - 15 January 2004. We made a breach of ~ 1.5 mm in the trail at a measured distance from the nest. We measured the time at which the first soldier appeared at the breach (discovery time), the time elapsed after discovery before the first worker deposited carton (recruitment time), the subsequent number of carton deposits per minute to repair the breach (building rate), and the time until the breach was repaired (completion time), to a maximum of 15 min. We performed these measurements twice on each nest, once on each of two consecutive days (at the same time). On one day, the breach was dampened with water (~ 2 mL) every minute, and the other day was a control. Treatment and control were applied in randomized order. This matched-pair design standardized for differences in rebuilding rate due to differences in colony traits.

RESULTS

The time until trail breaches were discovered by *N. corniger* was unaffected by water additions (mean ± SE = 29 ± 7 vs. 53 ± 18 seconds for control vs. water addition; paired-t = 1.26, df = 18, P = 0.89). With the addition of water, recruitment time was longer (paired-t = 3.31, df = 18, P < 0.004; Fig. 1) and building rate was faster (paired-t = 6.71, df = 18, P < 0.001; Fig.1). Consequently the total time to repair trail breaches

was longer in the presence of water additions (mean ± SE = 900 ± 0 vs. 692 ± 44 seconds; paired t = 4.70, df = 18, P < 0.001). Building rate was unrelated to distance from the nest in the absence of water (P = 0.12; Fig. 2), but increased with distance from the nest with the water addition treatment (r^2 = 0.44, df = 18, P = 0.002; Fig. 2).

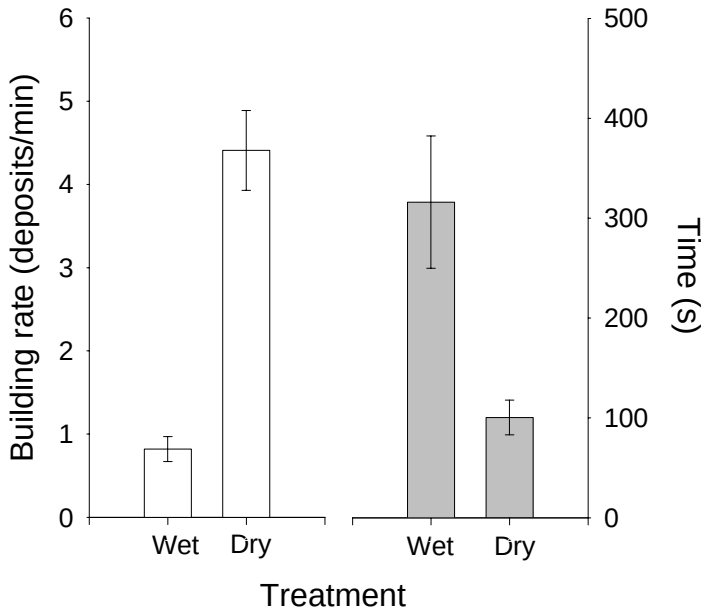

Figure 1. The rate (left) at which *N. corniger* rebuilds disturbed trails in wet and dry conditions and the time between when *N. corniger* soldiers discover a disturbance and when they recruit builders to fix it in wet and dry conditions (right). Mean (± SE) of rates and times are reported.

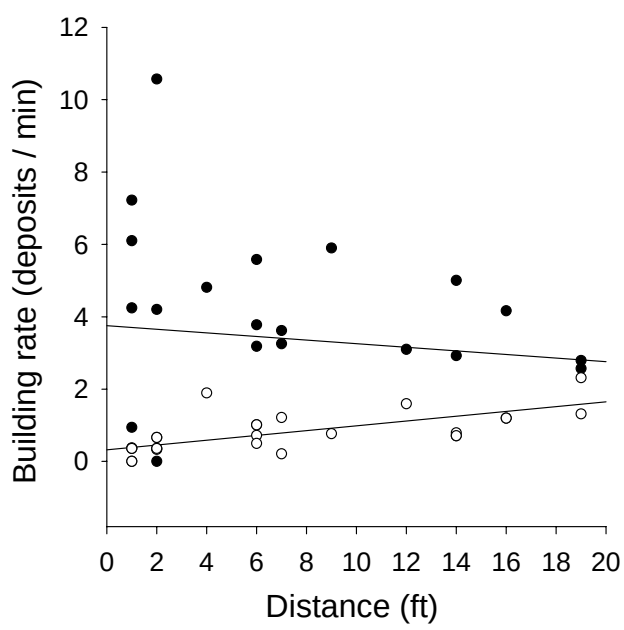

Figure 2. The rate at which *N. corniger* rebuilt trail breaches versus distance between the breach and the nest in wet (open circles) and dry (closed circles) conditions. Regression line shown for wet conditions.

Discussion

Our prediction that termites will rebuild trail breaches faster under wet conditions because water presents a threat was not supported. This suggests that trails are built for reasons other than protection from rain. We suggest three alternative hypotheses to explain why *N. corniger* builds protected trails.

First, termites may not build trails as protection from rain, but to preserve a more humid microclimate. Our wet treatment may have preserved the optimal level of humidity within the trail, so rebuilding quickly was not necessary to prevent desiccation. Altering the humidity without adding water could test this alternate hypothesis.

Another explanation could be that trails are built to protect against predation. For example, a soldier may generate alarm signals (presumably a pheromone) if the threat, like the continual application of water, remains present after the initial breach. This alarm signal may repel vulnerable soft-bodied workers and attract large-jawed, unpalatable soldiers (Lubin 1983). If the water addition treatments generated a sustained alarm, it could have caused recruitment time to increase and building rate to decrease, as we observed. This could also explain our finding that, under wet conditions, building rate increased as distance from the nest increased. A breach farther from the nest may pose less of a threat to the colony and would therefore be less likely to cause an alarm. This could explain the increase in building rate with increasing distance from the nest in the water addition treatment. Breaching trails at varying distances from the nest under both treatments

and counting the number of soldiers that appear at the breach could test this possibility.

Finally, the water-insoluble trails could specifically protect water-soluble communication pheromones from rain (Gribble, pers. comm.). The wet treatment could have diluted or altered the activity of pheromones that trigger repair behavior. Applying a treatment that disrupts pheromones without altering the microclimate could test this hypothesis.

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