

**Determination of Trophic Interactions Among Western Drywood
Termites, with the Intention to Develop an Effective
Bait for Control**

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Executive Summary

Differences in feeding and trophallaxis among castes of the western drywood termite, *Incisitermes minor* (Hagen), were determined using rubidium (Rb) as a tracer. Both 3rd- and 4th-instar larvae and 5th- and 6th-instar nymphs fed directly on Rb-treated paper and acted as both donors and recipients in trophallactic exchanges with other larvae and nymphs, and as donors for soldiers and alates. Soldiers and alates did not feed on Rb-treated paper suggesting that they do not directly feed on wood and are dependent on larvae and nymphs for their nutritional needs. Larvae paired with Rb-fed nymphs received the greatest amount of Rb suggesting that there may be a hierarchy of trophallaxis in drywood termites. Transfer efficiency, the percentage of total RB intake of donors passed to recipients, ranged from 1.1% (nymphal donors to alate recipients) to a maximum of 16.6% (larval donors to nymphal recipients).

Introduction

The western drywood termite, *Incisitermes minor* (Hagen), is an important wood-destroying pest in California, especially southern California. It is also in Arizona. The most comprehensive review of the biology of *I. minor* was published over 60 years ago in C. A. Kofoid's classic text, Termites and Termite Control. In the last ten years there has been some additional research on physiological ecology (Rust et al., 1988; Cabrera and Rust, 1992; Cabrera and Rust, 1994a; Cabrera and Rust, 1994b; Cabrera and Rust, 1996), caste development (Atkinson, 1993, unpublished), and control (Lewis, 1996; Rust et al. 1997). Although an economically important pest, however, there has been very little published scientific literature concerning its biology, behavior, or control. This study

attempts to determine whether or not baiting for control of drywood termites may be feasible. Passage of food between individuals in a drywood termite colony has been speculated, but not documented. Limited trophallaxis implies limited, but not necessarily impossible control via baiting.

Trophallaxis, the exchange of stomodeal or proctodeal material between individuals within the colony (Wilson, 1971), is a characteristic behavior of termites and other eusocial insects for maintaining colony homeostasis. It is important for termites because (1) it is the way newly molted individuals become re-inoculated with symbiotic, cellulose-digesting protozoans (McMahan, 1969), (2) it is the means by which pheromones, which regulate differentiation into the various castes, are distributed through the colony (McMahan, 1969; Moore, 1969), (3) it is how young larvae, soldiers and non-foraging colony members receive their nutrition (McMahan, 1969), and (4) it may be used for the distribution of moisture between colony members, especially for Kalotermitids, during periods of water stress (Collins, 1991). Trophallaxis may also occur with colony inquilines such as termitophilous beetles (Wilson, 1971).

The functional roles of the various castes in the western drywood termite, *Incisitermes minor* (Hagen), can be inferred from what is known in other termite species, but remain undetermined. Observations of *I. minor* during numerous experiments have led to questions on the types of interactions and behaviors that are specific to each caste. For example, preliminary studies indicate that *I. minor* alates do not feed directly on wood, an observation made in other termite species (Alibert, 1959, 1963). Therefore, it is likely that the nymphs are largely responsible for the care and maintenance of alates. However, there is little information on the feeding habits and trophallaxis of *I. minor*.

Studies on feeding and trophallaxis are needed to provide a better understanding of how *I. minor* is able to survive in xeric habitats and possibly how foraging and brood care is delegated within the colony.

Trophallaxis and feeding have been studied in several termite species using radiolabeled chemical isotopes. McMahan (1966) used Co^{57} and found that the size of *Cryptotermes brevis* nymphs had no effect on the direction or extent of trophallaxis. She also showed that trophallaxis was efficient in distributing substances within the colony as demonstrated by the acquisition of radioactivity in groups of up to 200 termites after the introduction of a single, radiolabeled nymph. Similar results were obtained by Afzal (1983) who detected a rapid spread of I^{131} throughout groups of 10 to 100 *Bifiditermes beelsoni* nymphs and by Spragg and Paton (1980) who reported rapid transfer of LA^{140} throughout colonies of *Mastotermes darwiniensis*. Alibert (1963) found differences in the substances that were exchanged by the African subterranean termite, *Cuibitermes fungifaber*. Preswarming alates and white soldiers received salivary secretions while adult soldiers and workers received regurgitated food. These studies give an indication of how homeostasis (e.g., caste ratio regulation, colony survival and growth) can be efficiently maintained within a termite colony.

Non-radiolabeled rubidium (Rb), an alkali metal found in trace amounts in insects (Van Steenwyk, 1991), was used to study feeding in the Formosan subterranean termite, *Coptotermes formosanus* (Chen and Henderson, 1994). It was an excellent marker because ingestion of Rb did not have an adverse effect on survival of nymphs at concentrations between 1000 and 5000 ppm, was not immediately excreted and was retained in the tissues at detectable levels for up to two weeks. Rb has also been used in

a variety of insect feeding and dispersal studies (Van Steenwyk, 1978; Holbrook et al., 1991; Holbrook, 1995; Corbett et al. 1996; Woods and Streett, 1996a,b; Coll et al., 1997; Woods et al., 1997).

The objectives of our research on trophic interactions in the western drywood termite were as follows: 1.) to determine if there were caste differences in feeding, 2.) to determine if alates received all of their nutritional needs via trophallaxis, 3.) to determine which castes act as donors in trophallactic exchanges, and 4.) to determine if larvae act as donors in trophallactic exchanges.

Materials and Methods

Termites.- Drywood termite-infested wood was collected in Riverside Co., CA, cut into sections and placed in Berlese funnels. Termites collected from glass jars attached to the funnels were placed on metal trays and covered with damp paper towels. The termites aggregated on the towels which were then placed, standing up, on Douglas-fir wafers lying inside plastic containers. The termites moved onto the wood, and those remaining on the towels were transferred with a fine camel's-hair brush. The containers were stored in the dark at ambient room temperature (approx. 23°C) for at least 7 d to ensure that only healthy individuals would be used for experiments.

Caste feeding.- The terms nymphs and larvae used in this report are those defined by Thorne (1996), larvae being immature instars 3 and 4 and nymphs designated as being instars 5 and 6. Both castes are non-reproductives, with the former having external wing buds and the latter without. Disks of filter paper (9 cm, Whatman International Ltd., Maidstone, England) were soaked in approximately 100 ml of aqueous RbCl solutions

with 1000, 2500, 5000 or 7000 ppm Rb and dried on a sheet of wax paper in a fume hood. Disks soaked in deionized water served as controls. After drying, the disks were placed in plastic petri dish lids (11 cm diam.) and moistened with 3 drops of deionized water. Groups of 10 alates (non-swarmling, mixed age), nymphs (5th- and 6th-instars), or larvae (3rd- and 4th-instars) or of 7 soldiers were placed on the disk and the dishes were covered, sealed with Parafilm[®], and placed in the dark at approx. 23°C. Groups of a single instar were not used because it was logistically difficult and time consuming to obtain sufficient numbers of a single instar and because of variation in individual sizes, which makes it difficult to distinguish between them. Nutrition, environmental conditions, health status, and irregular molting in the nymphs contribute to this variation. After 3 d, the termites were removed from the filter paper and transferred to plastic petri dishes (3.5 cm diam.), frozen at -55°C, placed in a desiccator containing anhydrous CaSO₄ (Drierite), and dried at 80°C for 24 h. The dried termites were held in the desiccator at ambient temperature for at least 12 h, weighed individually to the nearest 0.1 mg, placed in 20 ml scintillation vials (Kimble Glass, Inc., Vineland, NJ), and digested in 0.8 ml of 70% nitric acid. After 24 h, 0.2 ml of 70% perchloric acid were added to each vial and the contents were heated for 20 min to approx. 120°C. After cooling, 20 ml of deionized water were added to each vial and the contents were analyzed for Rb by inductively-coupled plasma-mass spectrometry (ICP-MS) (Perkin Elmer Elan 5000 with autosampler, Perkin-Elmer, Toronto). The total amount of Rb in each vial was measured, recorded as ppb Rb and divided by the dry weight (in mg) of the termites in each sample (ppb Rb/mg dry wt. of termite) to standardize for the differences in average weight of each caste. This final value gave a standard measure of termite feeding

activity. All analyses were replicated 3 times. Data were $\log(Y + 1)$ transformed and differences in Rb uptake among the castes for each concentration were analyzed by ANOVA with means separated using Tukey's HSD. A two-way ANOVA was used to determine the effects of caste, concentration, and the interaction between these two variables on Rb uptake. Data were analyzed using SAS (PROC GLM, SAS Institute, 1985)

Trophallaxis.- Ten larvae (3rd- and 4th-instars) or 10 nymphs (5th- and 6th-instars) were confined for 3 d to disks of filter paper treated with 7000 ppm Rb (donors) and allowed to feed as described in the feeding study. Control donors consisted of larvae and nymphs fed on disks of filter paper soaked in deionized water. Concurrently, the recipients (groups of 10 larvae, nymphs, alates or of 7 soldiers) were held separately in individual metal cylinders (4.5 cm high x 8.4 cm diam.) with a 40-mesh brass screen covering the bottom. First- and 2nd-instars were not used because of insufficient numbers and because they will often fall through the mesh screening. The cylinders were inserted into plastic petri dish bottoms (10 mm diam.) and the whole unit was kept at 21.1°C inside a plastic ice chest containing a saturated NaCl solution to maintain 75% RH (Winston and Bates, 1960). After 3 d, the Rb-fed donors were removed from the Rb-treated filter paper, placed together with the recipients, and the cylinders were placed inside the ice chests for 3 d. Any frass produced by the termites fell through the screen into the petri dish bottom below thus preventing the recipients from feeding on the donor's Rb-contaminated frass. Control donors were placed with their respective recipients and these groups were also stored in the ice chest. If the donors and recipients

were of the same caste, the two groups were marked on the abdomen with one of two colors (DecoColor, Uchida of America Corp., Carson, CA) to distinguish between them. Controls were similarly marked. At the end of 3 d, donors and recipients were separated and prepared for ICP-MS analysis. The amount of Rb in the donors and recipients (ppb/mg dry wt. termite) was compared with their respective controls with a paired t-test (PROC TTEST, SAS Institute, 1985).

Transfer efficiency. The Rb content of the controls from both the caste feeding and trophallaxis studies were pooled and the mean background Rb count of each caste was subtracted from the total Rb content of both respective donors and recipients to obtain the final Rb content per termite. Transfer efficiency (TE), expressed as the percentage of Rb in the donor that was transferred to the recipient, was calculated as

$$[R/(D + R)] \times 100$$

where R = the final Rb content of the recipient and D = the final Rb content of the donor. The percentage data were arcsine transformed and differences among the mean TE for each donor/recipient combination were tested for significance by ANOVA and means separated with Tukey's HSD (PROC GLM, SAS Institute, 1985).

Results

Background Rb levels. Mean background levels of Rb (ppb/termite \pm SD) determined from the pooled controls of the feeding and trophallaxis studies were 1.51 ± 0.995 (n = 21), 1.48 ± 0.603 (n = 21), 2.07 ± 1.261 (n = 9) and 1.44 ± 0.334 (n = 9) for larvae, nymphs, soldiers and alates, respectively. The corresponding mean dry weights (mg \pm

SD) for all control larvae, nymphs, soldiers and alates were 1.39 ± 0.255 , 4.49 ± 0.609 , 5.81 ± 0.953 and 3.79 ± 0.971 , respectively.

Caste feeding. There were no significant differences in mortality between *I. minor* nymphs fed on the 4 concentrations of Rb and nymphs fed on filter paper soaked in deionized water (Cabrera, unpubl. data). Caste, concentration, and their interaction had significant effects on Rb uptake in *I. minor* ($F = 77.56$, $df = 19, 40$; $P = 0.0001$). Within each concentration, nymphs and larvae confined for 3 d on Rb-treated filter paper had a significantly higher Rb content than did alates and soldiers at 1000 ($F = 26.9$, $df = 3, 8$; $P = 0.0002$), 2500 ($F = 105.9$, $df = 3, 8$; $P = 0.0001$), 5000 ($F = 35.46$, $df = 3, 8$; $P = 0.0001$), and 7000 ppm ($F = 156.2$, $df = 3, 8$; $P = 0.0001$)(Table 1) suggesting that larvae and nymphs are actively feeding on the treated filter paper. Alates exposed to 7000 and 5000 ppm Rb-treated paper had a significantly higher Rb content than the controls whereas the concentration of Rb of soldiers did not increase significantly. As expected, the larvae and nymphs acquired greater amounts of Rb as the concentration of Rb in the filter paper that they fed on increased (Table 1).

Trophallaxis. The Rb content of larval and nymphal donors varied from 19 to 68 ppb/mg dry wt. which was significantly higher than the controls. All recipients paired with Rb-fed donors had a significantly higher Rb content than recipients paired with control donors (Table 2). Larval recipients paired with nymphal donors had the highest Rb content (6.78 ± 4.855 ppb/mg) while alate recipients paired with larval donors had the

lowest (0.74 ± 0.185 ppb/mg). Results of the trophallactic exchanges examined in this study are summarized in Figure 1.

Transfer efficiency. Significant differences were found in the transfer efficiency between nymphal and larval donors and their recipients ($F = 12.02$, $df = 7$, $P = 0.0001$). Transfer efficiency (\pm SD) from larva to nymph was greater than from nymph to nymph (16.6 ± 0.83 % versus 3.1 ± 0.16 %). There was no significant difference in TE between nymphs and larvae (7.5 ± 2.77 %), larvae and larvae (6.8 ± 1.16 %), nymphs and soldiers (8.8 ± 5.70) and larvae and soldiers (8.9 ± 2.21). Transfer efficiency was lowest from larvae to alates (1.8 ± 0.35 %) and nymphs to alates (1.1 ± 1.10 %). Rubidium content among all nymphal donors was not significantly different although nymphs paired with larval recipients had more than twice the Rb content of nymphal donors that were paired with nymphal recipients (334.5 vs. 144.0 ppb/termite).

Discussion

Stimmann (1974) considered an insect marked if its Rb content was more than the mean endogenous Rb content plus 3 standard deviations (SD). The marked background levels of Rb (± 3 SD) for the controls pooled from both the feeding and trophallaxis studies were 0.70, 1.99, 1.34 and 0.59 ppb/mg dry wt. for nymphs, larvae, soldiers and alates, respectively. Larvae and nymphs acquired a marked level of Rb. Soldiers in this feeding study did not acquire a marked level of Rb because they could neither feed directly nor groom themselves because their mandibles are specialized for defense. Levels of Rb in the alates could have been acquired through external contact with Rb-treated surfaces and

subsequent ingestion during grooming. The other possibility is that they fed, but much less than nymphs and larvae.

The significantly higher Rb concentration of larvae and nymphs indicates that these are the castes of *I. minor* that feed. In fact, the amount of feeding by these two castes is similar on a per dry weight basis. Feeding by 1st- and 2nd-instar larvae was not examined. They may not be able to feed on wood or even on filter paper because their mandibles and associated musculature are probably not well developed. In most termites, young larvae do not feed directly (Grassé and Noirot, 1945; McMahan, 1969; Noirot and Noirot -Timotheé, 1969). LaFage and Nutting (1978) found that the older larvae, pseudergates and young nymphs in the Kalotermitidae are independent castes, i.e. can feed themselves, while young larvae, soldiers, older nymphs, the primary reproductives and, perhaps, unflown alates obtain their nutrition from the independent castes.

The assumption is made that feeding behaviors and responses in regard to trophallaxis are similar for 3rd- and 4th-instar larvae and for 5th- and 6th-instar nymphs. However, other factors besides the stage of development such as size, individual health, nutritional value of the wood, and environmental conditions, would make it very difficult to prove differences in feeding and trophallaxis between instars within castes with absolute certainty. Consequently, we took a more conservative approach by determining differences between castes rather than between instars.

Rubidium uptake by the larvae and nymphs versus the Rb concentration of the filter paper was non-linear for larvae between 1000-2500 ppm and for larvae and nymphs between 5000-7000 ppm Rb (Table 1). Several possibilities may account for these results. At lower concentrations and depending on the caste, the ingested Rb may flow

through the alimentary canal with very little uptake occurring in the hindgut. However, there may be a threshold concentration above which Rb is absorbed through the gut wall, enters the hemolymph and is then actively concentrated in the tissues. Additionally, high concentrations of Rb in the food substrate may lead to an increased metabolism which would lead to an increase in feeding. This is one possible effect of using Rb in arthropod feeding studies that should be investigated.

Trophallactic exchanges in *I. minor* occurred between starved larvae, nymphs, soldiers and alates and Rb-fed larvae and nymphs. Larval recipients paired with Rb-fed nymphal donors had a substantially higher Rb content than all other recipients (Table 2). Thus, the nymphs may be the primary donors within the colony and a hierarchy of recipients may exist with the larvae being the primary recipients. Conversely, larvae may be more active in soliciting from nymphs. However, because they are smaller and weaker than nymphs, it seems more plausible that they would be actively fed by the nymphs. Alates might be fed more often and require more care prior to and during swarming periods simply because the proportion of alates within the colony becomes increasingly larger.

One final factor to consider is that Rb may have been obtained by the recipients through cannibalism or the eating of exuviae - a very common behavior in termites. There was no evidence of cannibalism in any of the experiments but since we left the termites together undisturbed for 3 d, there was a remote possibility that exuviae could have been consumed.

Su and LaFage (1987) found that the subterranean termite, *C. formosanus*, soldiers were passive recipients, never soliciting and often refusing food offerings.

Worker to worker exchanges were more common than from worker to soldier. However, trophallaxis between workers and both alates and larvae was not studied; therefore, it remains to be seen if it is exclusively worker-initiated in this species. LaFage and Nutting (1978) explained that in the drywood termite, *K. flavicollis*, 3rd- and 4th-instar larvae and 1st-instar nymphs were the most active in reciprocal food exchange and as general donors to the dependent castes. First- and 2nd-instar larvae are rarely solicited while soldiers and active last-instar nymphs are poor donors.

Chen and Henderson (1994) attributed the variation in the Rb content of *C. formosanus* soldiers kept with Rb-fed workers to differences in the willingness of workers to feed soldiers and/or in solicitation behavior by the soldiers. LaFage and Nutting (1978) reported the observation by Alibert (1968) that *K. flavicollis* individuals are extremely attractive during the molting period and are solicited for proctodeal trophallaxis more frequently. Starving the recipients in our experiments was done to stimulate trophallaxis although we do not know whether the donors or the recipients initiated the interaction. Further studies of trophallaxis in *I. minor* could provide information on how readily material is offered by donors when solicited by recipients, if donors or recipients initiate trophallaxis or if it is a reciprocal interaction, and whether there are differences among the castes in the persistence, frequency or aggressiveness of the solicitation behavior of recipients, i.e. which castes are better solicitors.

Whether trophallaxis is stomodeal or proctodeal depends upon the recipient and the type of solicitation. Su and LaFage (1987) described stomodeal donations as a disgorging reflex caused by tactile stimulation of the donor's head and mouthparts by the solicitor's antennae and mouthparts. Similar stimuli applied to the posterior of the

abdomen result in proctodeal donations (McMahan, 1969; LaFage and Nutting, 1978; Su and LaFage, 1987). Observations of water-stressed *I. minor* nymphs revealed that proctodeal trophallaxis occurred when the recipient grabbed hold of the donor's abdomen with the mandibles and labial and maxillary palpi (Cabrera, pers. obs.). Sometimes the solicitor aggressively maintained its hold after the donor no longer appeared to be a willing participant. Similar observations were made by McMahan (1963) with *C. brevis*.

Transfer efficiency of the total amount of Rb per individual donor was low, ranging from 1.1 to 16.6 percent. We would expect TE to be low because Rb, with similar properties to K^+ (Van Steenwyk, 1991), is probably readily absorbed and assimilated into the tissues. However, the amount of Rb remaining in the alimentary canal was not determined; therefore, information on total ingested Rb, percent incorporation of Rb into the hemolymph and tissues and the rates of Rb absorption through the gut and excretion by donors, recipients and different castes was not determined. In addition to losses due to assimilation by the donors, trophallaxis with other recipients would also lower TE. Such exchanges would involve the passing of a more diluted material with a lower Rb content. Both McMahan (1966) and Afzal (1983) observed this phenomenon as the amount of radioactivity per individual decreased with increasing group size. McMahan (1963) calculated the percentage of the original counts per minute of radioactivity in donor nymphal powderpost termites, *C. brevis*, nymphs that was lost to the recipients and found that large nymphal donors lost 4.8 - 9.5% and small donors lost 10.3 - 16.9% of their radioactivity; these values are in close agreement with our results.

The low TE from nymph to nymph can be partially attributed to the low Rb uptake of the nymphal donors resulting in less Rb available for transfer. Perhaps these donors were in below-average condition and therefore, in addition to feeding less, were also poorer donors. Starved nymphs could also have solicited from fellow recipients both before and after mixing with donors. Thus the addition of the donors may not have made a difference such that the recipients were no more inclined to engage in trophallaxis with them than fellow recipients. Dilution of the Rb content in the recipients would occur as they engaged in trophallaxis with each other. The low transfer efficiency from both nymphal and larval donors to alate recipients, together with our results showing that alates do not feed directly, suggests that *I. minor* alates acquire the majority of their nutrition during the nymphal instars.

One common problem in feeding and trophallaxis studies in which tracers are used is the tremendous variability of the results (Afzal, 1983; McMahan, 1963, 1966). Variation in tracer uptake could be due to variation in the number of hindgut symbionts, which can also accumulate tracers, among individual termites (McMahan, 1966). Additionally, heterogeneity in tracer uptake reflects variation in the feeding of individual termites due to age, caste and the effects of molting (McMahan, 1969). Preliminary work for this study involved the detection of Rb in individual *I. minor* nymphs and revealed a great deal of variation in Rb uptake indicating variation in feeding.

The results of this study contribute new information on feeding relationships in *I. minor* and provide ideas for further research. The development of baits for use in controlling drywood termites would necessitate studies on the flow of material through a colony. This could provide information on how fast a toxicant is distributed within a

colony and whether toxic doses could be delivered to all colony members. Further work is planned to determine whether certain castes are fed by trophallaxis more than others, the ability of alates to act as donors, and the time for passage of food through the alimentary canal.

The flow of nutrients and food, trophallaxis, is a much slower process in drywood termites than it is in ants. A maximum of 16% of the Rb consumed was transferred from donors to recipients within 3 d. Consequently, only extremely slow-acting toxicants (insect growth regulators) that require small dosages will be effective as a bait against drywood termites. Secondly, the toxicant must not interfere with the metabolism of food and production of the fluids passed during trophallaxis. The development of a bait against drywood termites would be extremely useful because of their cryptic nature and the fact that many infestations are not entirely accessible for other conventional treatments.

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Table 1. Differences in feeding among castes of *I. minor* as measured by Rb content after feeding on filter paper containing various concentrations of Rb.

Caste	Mean ppb Rb/mg dry wt. of termite (\pm SD) [†]				
	Rb concentration of filter paper				
	Control	1000	2500	5000	7000
Nymph	0.3 \pm 0.1 a	11.4 \pm 3.6 a *	31.4 \pm 17.8 a *	47.6 \pm 23.7 a *	122.8 \pm 64.4 a *
Larva	0.6 \pm 0.3 a	9.3 \pm 4.8 a *	39.9 \pm 7.1 a *	36.2 \pm 7.9 a *	108.3 \pm 20.2 a *
Alate	0.4 \pm 0.06 a	0.8 \pm 0.04 b *	1.5 \pm 0.6 b *	4.7 \pm 3.8 b *	4.0 \pm 0.7 b *
Soldier	0.3 \pm 0.06 a	0.5 \pm 0.1 b	0.5 \pm 0.03 b	0.80 \pm 0.2 b	1.2 \pm 0.1 c

[†] ANOVA performed on log (Y+1) transformed data; Means within columns followed by the same letter are not significantly different.

* indicates acquisition of marked level of Rb according to Stimmann (1974).

Table 2. Comparison of Rb content between nymphal or larval donors feeding on Rb-treated filter paper (7000 ppm) with nymphal, larval, alate or soldier recipients after 3 days.

Treatment	Donor	Mean Rb content \pm SD (ppbRb/mg dry wt.)	Rb donor vs. control donor	Recipient	Mean Rb content \pm SD (ppbRb/mg dry wt.)	Rb recipient vs. control recipient
Rb	Larva	25.94 \pm 11.776	*	Larva	2.81 \pm 0.548	*
		55.59 \pm 16.228	*	Nymph	3.10 \pm 0.738	*
		53.90 \pm 29.44	*	Alate	0.74 \pm 0.185	*
		42.07 \pm 11.402	*	Soldier	1.43 \pm 0.398	*
Control	Larva	2.19 \pm 1.564		Larva	1.46 \pm 0.033	
		0.88 \pm 0.365		Nymph	0.24 \pm 0.022	
		0.81 \pm 0.118		Alate	0.39 \pm 0.056	
		0.91 \pm 0.150		Soldier	0.25 \pm 0.060	
Rb	Nymph	67.78 \pm 31.124	*	Larva	6.78 \pm 4.855	*
		19.09 \pm 12.526	*	Nymph	1.38 \pm 0.500	*
		66.38 \pm 25.267	*	Alate	2.16 \pm 2.035	ns
		45.29 \pm 12.238	*	Soldier	5.32 \pm 3.820	*
Control	Nymph	0.46 \pm 0.118		Larva	1.12 \pm 0.093	
		0.35 \pm 0.048		Nymph	0.37 \pm 0.004	
		0.22 \pm 0.015		Alate	0.38 \pm 0.057	
		0.36 \pm 0.238		Soldier	0.61 \pm 0.524	

* indicates significant difference between Rb and control within each caste; student's *t*-test.

Table 3. Percent transmission of total Rb per termite via trophallaxis from donors confined to treated filter paper to recipients after 3 days.

Donor/Recipient pairing	Mean ppb Rb/termite (\pm SD)^a		% transfer efficiency ^{a,b} (\pm SD)
	Donor	Recipient	
Larva/Larva	38.2 \pm 13.50 c	2.8 \pm 13.50 b	6.8 \pm 1.16 bc
Larva/Nymph	68.2 \pm 20.85 c	13.8 \pm 4.99 ab	16.6 \pm 0.83 a
Larva/Alate	90.6 \pm 50.85 bc	1.6 \pm 0.99 b	1.80 \pm 0.35 cd
Larva/Soldier	60.7 \pm 17.64 c	6.2 \pm 2.84 ab	8.9 \pm 2.21 ab
Nymph/Larva	334.5 \pm 165.81 a	29.0 \pm 20.31 a	7.5 \pm 2.77 bc
Nymph/Nymph	144.0 \pm 46.82 abc	4.7 \pm 1.49 ab	3.1 \pm 0.16 bcd
Nymph/Alate	295.9 \pm 106.34 ab	4.2 \pm 5.28 ab	1.1 \pm 1.10 d
Nymph/Soldier	217.0 \pm 58.83 abc	20.0 \pm 13.83 ab	8.8 \pm 5.70 ab

^a means within columns followed by the same letter are not significantly different; $F = 12.02$, $df = 7$, $P = 0.0001$, Tukey's HSD. Results based on arcsine transformed data.

^b Transfer efficiency = Recipient Rb / (Donor Rb + Recipient Rb). Rb content determined by subtracting mean background Rb levels of controls from total Rb content of each sample.