

**The Effects of Temperature and Humidity on the
Movement of the Western Drywood Termite**

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Introduction Abiotic factors such as temperature, RH, and rainfall play an important role in the survival and distribution of insect populations, particularly termites. These three abiotic factors are important in determining the geographic distribution and the local occurrences of termite infestations (Kofoid 1934; Steward 1981, 1983; Reddy and Sammaiah 1991). In addition, these factors have been shown to affect foraging patterns of subterranean termites (Haverty et al. 1974, Jones and Nutting 1989, Reddy and Sammaiah 1991) and distributions within buildings (Williams 1976), living trees (Greaves 1964), shrubs (Rust et al. 1979), and mounds (Holdaway and Gay 1948).

Termites have developed many morphological, physiological, and behavioral adaptations to survive exposure to adverse temperatures and humidities in underground nests, mounds, living trees, moist and decaying wood, and sound, dead wood. In comparison with insects of the other major orders, termites have a relatively thin cuticle because of their cryptozoitic habits. This makes them far more subject to the detrimental effects of temperature and RH, primarily through cuticular water loss. Within the Isoptera, there is considerable variability in relative cuticular thickness, presence of cement layers, and amount of epicuticular lipids (Collins 1969). This variation exists not only interspecifically, but also intraspecifically between age groups and castes. Epicuticular lipids are especially important in insects because they retard cuticular water loss (Edney 1977).

Unlike subterranean termites, drywood termites do not have a refugium to which they can retreat when the ambient conditions become unfavorable. Because they live entirely within the wood that they infest, drywoods have developed several adaptations to better withstand environmental temperature extremes and fluctuations. Drywood termites, compared to subterranean species, have a thicker and more impermeable cuticle (Minnick et al. 1973), highly specialized rectal glands for the reabsorption of water from the feces, and a moderate to large body size to decrease the surface to volume ratio (Collins 1969). Pence (1956) observed a clumping behavior in nymphs during his study

of *I. minor* under dry conditions. He also observed them sealing themselves from the surrounding atmosphere with carton thereby creating their own microenvironment.

Smith and Rust (1993) found that the level of O₂ uptake in *I. minor* was much lower at higher temperatures compared with the western subterranean termite, *Reticulitermes hesperus* Banks. Lower O₂ consumption is indicative of decreased respiration and lower metabolic rates, thus reducing water loss rates from the spiracles under conditions of high saturation deficits.

The objective of this study was to quantify the behavioral responses of *I. minor* to these abiotic factors. The behavior of *I. minor* nymphs when placed on a temperature gradient and held under different combinations of temperature and RH was videotaped and analyzed.

Materials and Methods

Avoidance of light A series of experiments was conducted to determine if the behavior of *I. minor* was influenced by light. The peripheral edge of disks of Whatman #1 filter paper (9.0 cm) was sealed with paraffin to the bottoms of ten petri dishes. Each of the dishes was divided equally into a light side and a dark side by completely covering half of both the bottom and the cover of the dishes with black electrical tape. Control dishes contained filter paper but were not divided into a light and dark side. Instead, a line was drawn across the middle of the cover so that the area of the dish was divided into two equal sections, labeled "A" and "B". Fifteen middle- to late-instar nymphs were put into each dish and placed on a table with fluorescent or incandescent lighting ca. 2 m directly overhead. The dishes were numbered and randomly arranged under the light to account for any positional effects with respect to the angle of the light rays reaching the dishes. The number of termites on the dark (A) or light side (B) was counted at 15, 30, 60, 120, and 1440 min after the termites were placed in the dishes. The experiment was repeated with the dishes placed ca. 1.5 m under a red photographic darkroom light

(Kodak Utility Safelight Lamp, Model D and Kodak 2 Safelight filter, Eastman Kodak Company, Rochester, NY) equipped with a 25-Watt light bulb. Both experiments were run under ambient room conditions (20 ± 2 °C; 30 + 5% RH). The data were analyzed using a chi-square goodness of fit test with MSTAT (Micro Computer Statistical Program; Michigan State University, East Lansing).

Temperature gradient study The system used by Smith and Rust (1993) was modified to study the behavior of *I. minor* when placed on a temperature gradient and under different RH's (Fig. 1). The test apparatus consisted of a 68.0 x 12.1 x 0.7 cm aluminum bar supported on both ends by a cylindrical aluminum post (15.3 x 6.7 cm diam.). A 68.0 x 7.6 x 0.25 cm piece of balsa wood (Sig Mfg. Co., Montezuma, IA) was placed on top of the bar. To provide a dark contrast to aid in the observation of the termites, a dark surface was needed on the bar. Therefore, the top surface of the balsa wood was painted with black India ink and air dried. A 68-cm long Plexiglas dome with a 3.8 cm radius was used to cover the wood and enclose the system. The dome had four 1-cm diameter holes drilled into it. The first two were located on each end, the third was located in the top center of the dome, and the fourth one was 1.3 cm below the third hole.

To maintain specific RH's for the duration of the experiments, the same humidifying system employed by Smith and Rust (1993) was used. Compressed air was passed through a Nalgene bottle containing water and mixed with dry air in a second Nalgene bottle. This mixture was passed into a third bottle in which a relative humidity sensor (Model 882 tubular sensor, General Eastern, Woburn, MA) was inserted through a hole in the lid. The sensor was attached to a digital thermo-hygrometer (model 880, General Eastern) which gave a readout of the RH of the air coming out of the bottle. Tygon tubing from the third bottle lead to a flow meter which regulated the air flow at a constant rate of 2360 cm³/min. Tubing from the flow meter was connected to a brass fitting in the fourth hole in the dome - thereby introducing the humidified air into the arena. Three different RH's were used for this study: 10, 30, and 50%. These RH's were

used because the maximum RH within an artificial gallery inside of wood blocks held at room conditions was only 48%. The three RH's were obtained by regulating the mixture of saturated and dry air from the Nalgene bottles. Trials conducted on the cold gradient at these RH's were designated as C10, C30, and C50 while those on the heated gradient were designated as H10, H30, and H50. The RH underneath the dome was determined with a second RH sensor inserted through the hole in one end of the dome. Both of the end holes were plugged with rubber stoppers (#0) during the course of each gradient run. The stopper with the sensor was slit so that the wire from the sensor could fit through it and be connected to the thermo-hygrometer outside.

Heat was applied to the bar by wrapping a Cal-Cord heating coil (Glas-Col Company, Terre Haute, IN) controlled by a Thermolyne Type 45500 input controller (Barnstead/Thermolyne, Dubuque, IA) around one of the aluminum posts. Because aluminum is a very good conductor of heat, a linear temperature gradient was obtained along the length of the bar. The heat gradient was transferred by conduction to the balsa wood placed on top of the bar. Twelve temperature sensors (PT-6 Physitemp thermocouple sensors, Physitemp Instruments Inc., Clifton, NJ) were attached with thin strips of duct tape to the surface of the wood that was left uncovered by the plexiglas dome. The last 2 cm of each thermocouple wire were in contact with the wood surface to ensure a more accurate temperature reading. The sensors were placed along the length of the wood at 5.35 cm intervals to create eleven 5.35 x 7.60 cm equal-sized temperature zones on the balsa wood. The sensors were connected to a 12-channel digital scanning thermocouple thermometer (Model No. 92800-00, Benchtop 115V, Cole-Parmer Instrument Co., Chicago, IL) and temperatures were recorded hourly by a printer connected to the scanning thermometer.

The gradient apparatus was placed on the bottom of an uncovered white, wooden box and within a horseshoe-shaped poster board enclosure to help capture the maximum amount of light from the darkroom lamp to help illuminate the termites for recording

purposes. The other end was closed off by several wooden boxes on which the darkroom lamp rested at a 45° angle to the apparatus below. After both the desired temperatures and RH had been reached, fifteen middle- to late-instars with no external evidence of differentiation were introduced into the arena through the third hole in the dome via a stemless glass funnel. Immediately after the termites were introduced, the hole was sealed with a piece of clear plastic tape and the room lights were turned off, leaving only the darkroom light for illumination. The termites' activity was recorded with a closed-circuit surveillance camera (Panasonic Model WW-1450, Matsushita Communication Industrial Co. Ltd., Japan) equipped with a 16 mm lens (Model #JL1613AF, F1.13, Javelin Precision Optics, Japan). The camera was attached to an adjustable, telescoping mount (PhoenixTM Monopod, Model 02-050, Taiwan) that was fixed to the ceiling above the arena. Termite activity was recorded on videotape with a video cassette recorder (SL-2400, Sony Corp., Japan) specially modified to record for 5 min at the beginning of each hour for 24 hours.

The room temperature was kept as close to 21.1°C as possible. This was important because high and low ambient temperatures affected the temperatures on the aluminum bar. The experiment was periodically monitored so that the temperature in the room or on the bar could be adjusted. The same set-up was used for the cold gradient - the only difference being that no heating coil was used and one of the end posts was immersed in ice. A small ice chest had a 6.75 cm hole drilled through its lid, allowing the aluminum post to be inserted through it and into the chest. The aluminum post was immersed in tap water contained in a 1000 ml beaker packed in crushed ice inside the chest. Control runs were conducted on the aluminum bar held at $21.1^\circ \pm 2^\circ\text{C}$ so that the temperature throughout the length of the balsa wood did not differ from more than 0.5°C at most from one end to the other. Each of the experiments for hot, cold, and control gradients at each of the three RH's was replicated 5 times for a total of 45 temperature gradient runs. The dome was washed after each run with soap and water, dried and

rinsed with 80% EtOH to remove any semiochemicals from the termites that may have been deposited on it.

Analyses of the tapes were done as follows. Ten random numbers from 1 to 360 were selected which corresponded to each second of the 5-min recording period. A grid (40.3 x 6.3 cm) divided into eleven 3.66 cm zones was drawn with waterproof ink on a piece of clear acetate. The grid was superimposed on the television screen image of the top view of the balsa wood thereby providing a visual representation of the 11 temperature zones on the wood. When the videotape was placed on pause at the pre-determined time, the number of termites within each zone was counted. For each hour a total of 150 observations was made (10 counts of 15 termites). This was done hourly for each of the 24 h. The first five minutes of the experiment were not viewed for generating distributional data because the termites' behavior was affected by their initial introduction into the arena. Termites which died were not counted.

To determine the distributional patterns of the termites exposed to various temperature gradients and RH's, the number of termites within each zone for each hour during the 24-h period was totaled and an average number of termites per zone was determined. A grand mean ($n= 5$) for each zone was obtained and compared with the grand mean for the controls using a Kolmogorov-Smirnov test for goodness of fit (Conover 1971). A Kolmogorov-Smirnov two-sample test was used to determine if temperature or RH had a significant effect on the distributions of termites on the gradient.

To determine if the termites selected particular temperatures on the gradient at which to settle, a mean temperature preference value (mTPV), which represents the temperature at which the majority of the termites were found on the gradient, was calculated (Steward 1981, Smith and Rust 1993). It was calculated by multiplying the number of termites within each zone by the average temperature of that zone. The resulting values for each of the 11 zones were summed for each of the 24 hours and

divided by 150 (10 counts taken per 5-min period x 15 termites per count; this number was adjusted for any mortality). The grand mean of the mTPV's for each RH was compared with the grand mean coldest or hottest temperature on the gradient. The termites were said to be avoiding the hot or cold temperatures on the gradient if the mTPV was significantly different from these temperatures using the Wilcoxon signed-ranks test.

Because both daily and seasonal fluctuations in temperature affected the room temperatures in which the experiments were conducted, especially during the winter and summer, the actual gradient temperatures varied between and within treatments. Therefore, any differences by the termites in mTPV might result from differences between the temperature gradients. Consequently, the median bar temperatures (MBT) between and within all of the RH's and runs were compared to determine if they were significantly different from each other using a Kruskal-Wallis and Mann-Whitney U-test. The MBT is simply the temperature at the middle of the gradient and is essentially the same as the average temperature of the gradient.

The absolute value of the difference between mTPV and MBT ($|mTPV - MBT|$) was also used as a means of comparing temperature preferences. This value actually represents the distance of the termites from the middle of the bar. The larger the value, the further the termites are from either the cold or hot end of the bar. These values were analyzed using a Kruskal-Wallis and Mann-Whitney U-test.

Initial review of the raw data indicated that it took longer for termites to settle and aggregate on the cooler gradients than it did on a heated gradient. To see if this was actually occurring, the termites were first considered to be in an aggregation if 80% of them (120 of 150 observations) were within 2 adjacent zones. The number of hours required for aggregations to form in all 45 trials was determined and means were calculated for each of the 9 gradient conditions. The means were tested for significance using a Kruskal-Wallis and Mann-Whitney U-test.

All statistical analyses were performed on MSTAT (Micro Computer Statistical Program, Michigan State University, East Lansing).

Aggregation study Another series of experiments was conducted to determine if RH had a significant effect on the aggregation of *I. minor* nymphs. The peripheral edge of a disk of black construction paper was sealed to the bottom of a petri dish with paraffin and fifteen middle- to late-instars without external evidence of differentiation were placed in the dish. The dish was placed in a small desiccator containing saturated salt solutions of either lithium chloride, magnesium chloride or sodium dichromate to maintain RH's of 11, 32.5, or 55% RH, respectively (Winston and Bates 1960). The desiccator was placed inside of a small, empty ice chest and on top of a stack of plexiglas squares so that the lip of the desiccator was ca. 1 cm above the top edges of the chest. To heat the desiccator, the heating coil and equipment described previously was used. To obtain cold temperatures, the desiccator was placed inside the ice chest and packed in crushed ice. The desiccator was covered with a 20.3 cm diameter piece of plexiglass with a 1-mm hole located 3.5 cm from the edge. A thermocouple temperature probe (PT-6 Physitemp Thermocouple sensor, Physitemp Instruments Inc., Clifton, NJ) was inserted through the hole so that it extended ca. 5 cm into the desiccator. The termites were allowed to acclimate for three hours under the photographic darkroom light in the desiccator. The termites were recorded for 5 min using the same equipment described above except that the camera was equipped with an 8 mm lens (Panasonic Model WV-LA 8A, F1.1.4, Matsushita Communication Industrial Co. Ltd., Japan). Five replicates were used for each of the 3 RH's for both hot and cold temperatures.

The videotapes were analyzed as follows. One random number from 1 to 360 was selected as described previously. The videotape was paused at the predetermined time and an acetate sheet was placed on the video screen. A single termite on the screen was picked at random and the remaining fourteen termites were then numbered in ascending order according to their distance from the first termite using the nearest

neighbor technique described by Southwood (1966). A random number between 1 and 15 was selected, corresponding to the termite of the same number on the screen. Five additional numbers between 1 and 15 were randomly selected, excluding the first number already picked. The distances (cm) between the thorax of the first termite selected and the other five termites were measured. This procedure was repeated for each replicate so that 25 measurements were obtained for each treatment. The procedure is diagrammed in Fig. 2. Both the mean distance between termites and the mean cumulative distance for each treatment were calculated and tested for significance by ANOVA and the means were separated using Tukey's Honestly Significant Difference test. All statistical analyses were done on MSTAT.

Results and Discussion

Responses to Light *I. minor* nymphs exhibited a strong avoidance reaction towards incandescent and fluorescent light while they did not react to red light (Table 1). Within 15 min, 75 and 98% of the termites had moved to the shaded side when exposed to fluorescent and incandescent light, respectively. Only 55% were found on the shaded side under red light. Even though the nymphs are eyeless, they exhibited a strong negative phototaxis. This may partially explain why drywood termites will forage near the surface of the wood, leaving only a thin layer of wood or paint to cover their galleries.

The results of nymphs tested under photographic red light indicated that they tended to aggregate on one side or the other, but the observed frequency was not significant overall. Consequently, the temperature gradient and aggregation experiments were conducted under a photographic red light.

Responses to a temperature gradient The comparison of median bar temperatures (MTB) gave the following differences in bar temperature: C10 > C30 = C50; H10 > H30

= H50 (Table 2). The only significant differences in mTPV was between C10 and both C30 and C50. The mean mTPV's for C10, C30, and C55 were 21.7°, 19.2°, and 19.6°C, respectively; for H10, H30, and H50 they were 31.4°, 31.2°, and 30.6°C, respectively. Thus, any differences between gradient temperatures at the different RH's generally did not affect the mTPV's.

I. minor nymphs showed a strong avoidance of hot and cold temperatures. There were significant differences between mTPV and the highest temperature on the heated gradient and mTPV and the coldest temperature on the chilled gradient at all 3 RH's. The differences between mTPV and the highest or lowest bar temperatures over 24 h are shown in Figs. 3-8. As the temperature of the bar increased or decreased because of changes in room temperature, there was a gradual, corresponding change in the mTPV. These mTPV's were not significantly different from one another. The graphs show that the termites respond rather quickly to the changes in temperature. As the temperature on the bar increased or decreased over time, the termites moved even further away from these extreme temperatures, suggesting some type of ongoing selective process (Figs. 9 and 10). The nymphs relocated in response to the changes in temperature on the gradient. This behavior was consistently observed with both the hot and cold gradients. However, another factor that must be considered is the presence of a humidity gradient. The RH at the heated end of the gradient at 50% RH was about 35%. At 10 and 30% RH, the RH's at both ends were nearly the same. The termites at H50 could be responding to a humidity gradient and different saturation deficits within the apparatus. It has been shown in other studies that termites have definite humidity preferences when placed in humidity gradients. Agarwal (1978) found that the workers and soldiers of *Odontotermes microdentatus* Roonwal and Sen-Sarma and *O. obesus* (Rambur) were mostly found in the areas of higher RH of a humidity gradient. He also found that the workers responded faster to the gradient of RH than did the soldiers. Steward (1982) studied the humidity preferences of five species of *Cryptotermes* using a circular gradient

and found differences due to species, colony origin, and pre-conditioning. Sen-Sarma and Chatterjee (1966) found that pre-conditioning had a significant effect on the reaction of *Microcerotermes beesonii* Snyder on a linear humidity gradient. Minnick et al. (1973) found that *Cryptotermes brevis* preferred a higher RH on a linear gradient. Yinon and Shulov (1969) found that the khapra beetle, *Trogoderma granarium* Everts, aggregated at both ends and were distributed more evenly in the absence of a humidity gradient but displayed a unimodal distribution at the low end of a humidity gradient.

The response of *I. minor* nymphs to temperature was probably greater than the response to RH as the gradient in RH was not very large, even at H50. Furthermore, comparisons of the distributions at different RH's showed that they were not significantly different from each other. Also, the aforementioned RH gradient studies were all conducted at uniform temperatures so the insects responses were due solely to the humidity gradients.

The differences between the quantity ($|mTPV-MBT|$) were significantly different at all 3 RH's for the cold gradients while in the heated gradients, the difference was significantly greater at H10 than both H30 and H50 (Table 2). *I. minor* nymphs at 10% RH, whether at high or low temperatures, had a greater difference in mTPV-MTB than they did at 30 and 50% RH. Since this value is basically a measure of the distance of the termites from the middle of the bar, the termites at 10% RH were found farther away from the hottest or coldest temperatures on the gradient than they were at 30 or 50% RH.

The behavior of *I. minor* nymphs was directly affected by temperature and analyses of the videotapes confirmed this. When the nymphs were first placed on the gradient, they usually dispersed in several directions. Individuals were observed approaching areas of ca. 44-47°C, stopping, and reversing their direction. On several occasions, individual termites came upon these areas very rapidly and as a result had walked into an area that they normally would have avoided if their approach had been slower. Once these individuals had detected these high temperatures, they sometimes

would run wildly in different directions, apparently becoming disoriented. Most individuals eventually were able to find areas of cooler temperatures, but several eventually succumbed to these high temperatures.

Avoidance behavior by individual termites was not as apparent on the cooler gradients. Individuals that ventured onto the coldest sections of the bar did not display an immediate avoidance response. Avoidance of the cooler areas became apparent after several hours when the individuals had aggregated in zones of the warmest temperatures on the gradient (Fig. 9). The temperature ranges that *I. minor* avoided consistently were in the range of 44° to 47°C on the heated gradient and of 12° to 15°C on the cold gradient. The higher temperatures have been reported during the summer from the center of various wood members of an attic and from wall studs in a building on the UC Riverside campus; the lower temperatures have been reported from late November (Rust and Cabrera, unpublished data). It is likely that colonies of *I. minor* relocate to areas within a structure of more hospitable temperatures in response to these temperature extremes.

Bursell (1974) stated that there are different optimal temperatures for different physiological functions in arthropods. Steward (1981) mentioned that, for instance, the optimal temperature for mating or oviposition may not be the optimal temperature for feeding. Feeding rate increases as temperature increases, but higher temperatures in combination with a low RH can cause an increased cuticular water loss leading to lower survival. The mechanisms by which insects select a particular temperature range are not completely understood. Insects do have temperature and hygroresponsive receptor neurons that enable them to detect temperatures and RH and these stimuli are processed by the nervous system - resulting in a reaction from the insect to either stay or move. These responses are probably instinctive, being influenced by environmental factors. Behavior may also be dictated by a gradual sensory awareness of uncomfortable temperatures. The termites on the gradient may be reacting in this manner as the temperatures get

warmer or colder, thus the aggregation moves to a cooler or warmer area (Figs. 9 and 10).

To say that insects have "preferred" temperatures would imply that they are making a conscious choice on where to move. The use of the term "preference" has been questioned (Chapman 1964, Youdeowei 1968) but by now the term is used as a matter of convention rather than for its actual implied meaning. Regardless of the terminology, the results clearly show that the termites settle at particular temperatures when placed on various temperature gradients.

In the first temperature gradient study with a drywood termite, Steward (1981) looked at the behavioral responses of four *Cryptotermes* species to temperature gradients and the effects of pre-conditioning on these responses. He found that the termites avoided temperatures $>35^{\circ}\text{C}$ (with the exception of one species) and were seldom found in the coldest areas. The preferred temperature ranges of the different species were unaffected by RH. Differences in the temperature preference range existed between species and between colonies within species from different geographic locations. Individuals pre-conditioned at 75% RH showed a higher temperature preference than those kept at 85% RH.

Smith and Rust (1993) found that on a heated gradient, *R. hesperus* had a mTPV of approximately $29\text{-}32^{\circ}\text{C}$. These values were always near the coolest temperatures of the gradients and were within the range we found for *I. minor*. Very few *R. hesperus* workers were ever found in sections of the gradient above 40°C which was also true for *I. minor* nymphs. On a steep gradient (ca. 6° to 40°C), *R. hesperus* workers preferred temperatures between approximately 14° - 19°C , slightly lower than the range of 19.2° - 21.7°C for *I. minor* on cold gradients. Smith and Rust (1993) also tested a greater range of RH's (20 to 90% RH vs. 10 to 50% RH) and found that RH did not have a significant effect on the mTPV. The percentage of termites in the coolest sections of the bar increased as RH decreased. Their explanation was that the termites retreated to areas of

lower temperature because of the lower saturation deficit (SD) in these areas. At a lower SD, cuticular water loss is reduced and, consequently, survival increased. This may be more important for *R. hesperus* than for *I. minor* because the cuticular permeability of the former species is much higher (19.2ug/cm²/hr/mmHg) than for the latter (2.5ug/cm²/hr/mmHg) (K. Haagsma, unpubl. data). Our results showed that the mTPV decreased only slightly if at all as RH increased and that these differences were not significant. In addition, the temperature gradients were slightly higher at 10% RH which may have also accounted for the slightly higher mTPV's at this RH.

Drywood termite nymphs tended to aggregate, even in the absence of a temperature gradient (Fig. 11). These aggregations occurred away from the hottest or coldest temperatures of the gradient (Figs. 9-10). Aggregations were also observed in drywood termites by Minnick et al. (1973) with *Cryptotermes brevis* and by Stewart (1981) with four species of *Cryptotermes*. Smith and Rust (1993) did not observe any aggregating in the rhinotermitid, *R. hesperus*, possibly because their experiments were conducted for only 2 h. The aggregations in *I. minor* consisted of all 15 individuals most of the time but there were instances where there were only 5-10 individuals formed in a group. It took a significantly shorter time for aggregates to form on the heated gradient (2.2 hours) than it did on the controls (8.67) or the cold gradients (4.87) (Table 3). Relative humidity did not have a significant effect, although it took about an hour longer for aggregates to form at 50% RH than at 10 or 30% RH. Aggregations formed faster on the heated gradients because *I. minor* nymphs may be more responsive to hot than cold temperatures. The nymphs were also more active at the higher temperatures. Therefore they could react quickly to unfavorable temperatures and form aggregations in less time whereas the reactions of the nymphs were slowed by the cooler temperatures. Nymphs on the controls had no unfavorable temperatures or temperature differentials to react to and so it took longer for them to aggregate. The nymphs have a natural tendency to

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aggregate and hot or cold temperatures can facilitate and accelerate the formation of these aggregations.

Additionally, the difference in responses to hot and cold temperature extremes on the gradients may not have been comparable. That is, while the temperatures on the heated gradient were often very hot (sometimes near 50°C), the low temperatures on the cold gradients were not especially cold (8°-10°C at the least but usually 12°-14°C). The problem was that it was difficult to get very cold temperatures on the balsa wood, owing to its physical properties, despite the fact that the bar at the cold end was 0°C.

The possibility of an "edge effect" affecting and overriding the insects' response to temperature on a linear gradient has been mentioned before by Östbye (1970), El Rayah (1970), and Minnick et al. (1973). Steward (1983) in his study with *Cryptotermes* spp. used a circular gradient to eliminate this factor. The controls that we used showed the same type of edge effect as Toyé (1970) observed with the dermestid *Dermestes maculatus* Degeer. However, the termites in our controls gravitated to either end of the bar, resulting in a bimodal distribution when the control data at each RH was pooled (Figs. 12-14). In all of the gradient runs, the termites always aggregated away from the hot or cold end - no matter which end of the bar it was. By comparing the actual distributions of the termites on the gradient, regardless of temperature and RH, the distributions of *I. minor* on both heated and cold gradients were significantly different from the controls (Figs. 12-14). Relative humidity had no significant effect on the distributions of termites within or between heated or cold gradients.

Analyses of the data coupled with their observed behaviors showed that the termites aggregated at one end because they were avoiding the high or low temperatures at the opposite end of the bar, not because of an edge effect. In fact, aggregations were not always found at the ends of the apparatus and some aggregations were found at surprisingly warm temperatures (35° - 38°C) located several cm away from the end.

Aggregation Based on the observed tendency of the termites to aggregate in our study even in the absence of a gradient, we determined if the intensity of aggregation as measured by the mean distance between termites within the aggregation was influenced by temperature, RH, or saturation deficit. Mean distance was significantly greater in the cold gradients (2.42 cm) than in the heated treatments (1.66 cm). Mean distance was greater at 55% RH (2.41 cm) than it was at 32% (1.64 cm) and 11% RH (2.08 cm) although they were not significantly different from each other. The mean distance was largest at C55 and this was significantly different from the other treatments. Overall, neither RH nor the interaction between temperature and RH had a significant effect (ANOVA $F= 1.53$, $df= 2$, $P= 0.24$; $F= 1.96$, $df= 2$, $P= 0.16$, respectively) but temperature did have a significant effect ($F= 4.36$, $df= 1$, $P= 0.05$)(Table 4). When the distances measured between termites for each replicate were summed, the mean total was larger in the cold temperatures than it was at the warm temperatures (36.30 cm vs. 24.96 cm). At higher temperatures the termites aggregated closer together probably due to a higher saturation deficit, not in response to RH. Pence (1956) proposed that aggregating closer together may reduce the amount of exposed surface area to cuticular water loss. Since this combination of cold temperature and higher RH was also the smallest saturation deficit, a regression was calculated to see if there was a correlation between saturation deficit and aggregation as measured by the mean distance between termites in the group. The result of this analysis was not significant ($r= 0.50$, $t= 1.14$, $P= 0.32$). There was a fair amount of variability in mean distance, especially at the lower SD's. Perhaps if the exposure time of the nymphs to the different experimental conditions were increased, then the distances between the nymphs might be less variable. The intensity of aggregation may also be influenced by the size of the group as well as by the caste and age composition of the group.

Trail following Another interesting observed behavior was that of a single individual (occasionally two) leaving the aggregation and proceeding towards the hot or cold end of the bar. If this occurred on a heated gradient, the individual often encountered an area where the temperature was too hot and then exhibited the avoidance behavior described previously. This behavior was sometimes very distinctive as it appeared that the termite had bumped into an invisible wall and could go no further. Occasionally, individuals would react with the same wild and animated movements as seen before. After retreating from this area the individual eventually returned to the group, frequently along or near the same path from which it had come. This suggested that the termites were using some cue to find their way back to the group - such as a trail pheromone. This may be important since no pheromone of any kind from *I. minor* has been isolated, identified, or bioassayed. Another explanation for this trail following behavior is that the individual might be detecting vibrations from the substrate as the termites feed at the other end or as they tap their heads on the substrate, another commonly observed behavior. However, if this were the case, then a more random path should have been observed on the termite's return. The return path could also be simply random and any apparent trail following could be a result of the narrow width of the enclosed gradient, thereby increasing the probability of the termite following the same path. It should be noted that not all return trips followed the same path as the one taken out. Some individuals started out using the same path but then deviated from it and in some instances they reached the side of the dome and returned to the group by following this edge. Several reasons support the idea that a trail pheromone is responsible. Trail pheromones are used by many different termite species and sternal glands, which secrete the trail pheromone, have been found in several species of kalotermitids (Noirot 1969). Another reason is that close trail following was observed on numerous occasions. In fact, during any 5-min taping period this type of behavior was often observed several times. Sometimes one or two termites would leave the group and return and shortly thereafter one or two other termites would

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leave the group and proceed on their own towards the other end. It is very likely that this behavior occurs periodically. Any proposed explanation for this behavior is teleological.

Obvious group trailing behavior has also been observed, especially during the first 5 min when the termites have just been introduced onto the gradient. In one particular instance, a group of termites was located in the middle of the gradient and one termite left and walked towards the heated end by taking a semi-circular path. It walked about three centimeters before it apparently detected an unfavorable temperature (ca. 45°C). At this point it immediately turned back and followed the same path back to the group. Upon returning, another individual proceeded to leave and walk towards the heated end following the same path that the first termite had taken. This termite reached the same spot as the first one, turned around and returned to the group along the same path. Another individual left and proceeded to repeat the same behavior as the first two termites. This behavior continued with five other termites. When the last one returned, the entire group left with all of the members of the group following the same semi-circular path in single file, stopping, and then moving back to a new location further away from the heated end. Group trailing behavior, though not as distinct as this example, was observed on several occasions in other replicates. In these instances, smaller groups of individuals were observed in single file moving to a location away from the hot or cold end.

The behaviors observed in this study could also be affected by several other factors such as group size. Youdeowi (1968) found that the distribution of groups of ten 4th-instar cotton stainers, *Dysdercus intermedius*, on a temperature gradient were unimodal and located in the middle of the gradient. The distributions of groups of 25 to 50 larvae were bimodal, with one group at the "preferred" temperature and the other at the cold end of the gradient. Fifth-instar larvae aggregated strongly below 20°C and began to scatter above 30°C. Yinon and Shulov (1969) found that the response of *Trogoderma granarium* to humidity gradients was stronger for groups than for

individuals. Langer and Young (1976) found that both *Tribolium confusum* and *T. castaneum*, selected higher temperatures on a hexagonal gradient as their density increased. It is possible that increased contact with other individuals and a modification of the immediate microenvironment by the presence of more or less individuals may affect the behavior and response of termites to the gradients.

Caste and age composition of the group may also affect termite responses. Steward (1981) found that *Cryptotermes dudleyi* reproductives showed a significantly lower temperature preference than pseudoworkers while in *C. brevis*, the preference for soldiers was similar to that of pseudoworkers. Pätzold and Ritter (1989) found that in the honey bee mite, *Varroa jacobsoni* O., the temperature preference range of old winter mites was narrower than for young summer mites.

It is apparent that any organism's responses to any given stimuli can be influenced by many factors such as the animal's physiological state, genetic make-up, the environmental conditions, the intensity of the stimulus, and the presence of other organisms. While all of these factors could not be controlled, this study shows that nymphs of *I. minor* avoid light and extreme hot and cold temperatures. They also respond to changes in temperature and have a tendency to aggregate in areas of suitable temperature. Trail following, both individually and in groups, gives further evidence for the use of a trail pheromone in this species. The information gained in this study provides further support for the idea that colonies of *I. minor* may relocate themselves within a structure in response to temperature changes. This information is important in expanding our knowledge of the behavior and biology of this economically important termite species. Knowledge of temperature preferences may improve the quality of termite inspections and applications of spot treatments or baits in the future.

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