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ABSTRACT

Atta cephalotes is one of the few species that does better in grassy pastures and secondary growth and their abundance, persistent foraging, and that they collect from a lot of different tree species has earned them the reputation of huge agricultural pests. *A. cephalotes* are poikilotherms meaning their internal body temperature fluctuates greatly with temperature. For this reason, it has been purported that these leaf-cutter ants will only collect leaf fragments at certain temperatures and that different sized workers have different temperature tolerances. The objective of this study was to look for relationships between temperature, productivity, and worker size in nests in Monteverde, Costa Rica. It was found that some nests' productivity was more responsive to changes in temperature and that nest and temperature interact to predict worker size during foraging. Because of *A. cephalotes'* large impact on the ecosystem in Monteverde (whether viewed as good or bad), it is important and interesting to know more about what regulates the speed of their foraging.

RESUMEN

Atta cephalotes es una especie que se dessrrolla mejor en pastos y bosques de crecimiento secundario. Su abundancia, forrajeo persistente, y el hecho que recolectan muchos tipos diferentes de árboles les da la reputación de grandes pestes agrícolas. *A. cephalotes* es una especie poiquilotérmica lo que significa que la temperatura interna de su cuerpo fluctúa con la temperatura ambiental. Por esta razón, se piensa que las hormigas que cortan-hojas solamente recogen fragmentos de hojas durante temperaturas especificas y que trabajadores de tamaños diferentes tienen tolerancias de temperature diferentes. El objetivo de este estudio fue entender las relaciones entre temperatura, productividad, y tamaño de trabajadores de esta especie en Monteverde, Costa Rica. Descubrí que la productividad de algunos nidos fue mas afectada por la temperatura que otros.También que temperatura e identidad del nido interactuan para predecir el tamaño de los trabajadores durante el forrajeo. Dado el impacto grande que tiene Atta cephalotes en los ecosistemas de Monteverde (si bueno o malo), es importante e interesante saber más de lo que limita y acelera el forrajeo.

INTRODUCTION

For social and poikilothermic insects such as the leaf-cutting ant *Atta cephalotes*, temperature affects development, phenology and foraging activity (Crist & Williams 1999). It has been suggested that there is a range of temperatures under which the *A. cephalotes* worker caste will forage. *A. cephalotes* is found throughout Costa Rica mainly in pastures or secondary growth (Hölldobler & Wilson 1990). These leaf-cutters are broadly polymorphic ants—the workers range in size from 2mm in length to 20 mm in length (with workers within a single colony possibly ranging 250-fold in mass) (Stevens 1983). In another species of thermophilic ants (*Cataglyphis velox*), it was found that thermal tolerance was size related with larger workers being able to withstand higher temperatures (Cerda & Retana 1997). It has been suggested that colony fitness is related to fungus production (which is related to foraging productivity). Additionally, another study on the army ant *Eciton burchellii* found that the ants retreated from warm edges, steered around hot patches in the forest, and appeared in many ways to be living near the upper limit of their temperature tolerance. This study also found that *A. cephalotes* was more tolerant of high temperatures than *E. burchellii* but still showed a negative response to temperature (Meisel 2006).

Atta cephalotes nests are very common in Monteverde, Costa Rica. The majority of the *A. cephalotes* nests in Monteverde are in the sun (in cleared pastures or young secondary growth). However, some nests are completely shaded. Also, the topographic locations of the nests are very varied. There is not much known about how the interaction between temperature and foraging is affected by topographic positioning, but it is clear that there is an effect.

Because *A. cephalotes* has this optimum temperature range that influences the number of foraging hours they have in a day, correlations between the productivity and thus fitness of *A. cephalotes* in the Monteverde area should be related to temperature. The goal of this study was to investigate the relationship between temperature and productivity as well as temperature and worker size in *Atta cephalotes.* The results were expected to show a peak and trough in foraging activity along a temperature range (productivity declining when it is too hot or too cold).

MATERIALS AND METHODS

STUDY AREA. —The study was conducted on three different *Atta cephalotes* nests within Monteverde, Costa Rica. Monteverde is classified as Tropical Lower Montane Wet Forest. Nest one is in an open pasture owned by Don Juan coffee company. The grass growing in the pasture is about one foot high and the nest is in full sun. Also, the nest itself is barely visible partly because of the grass but also maybe because a large part of it is underground. Nest two is in Bajo del Tigre in the Children's Eternal Rainforest. This nest seems has a very large obvious pile where the ants are discarding. Nest three is on private property in Cañitas. This nest is also in an open pasture but the grass here is much shorter. This nest appears to be significantly younger than the other two judging from the size of the nest. Nest two in Bajo del Tigre is at 1300m elevation and the other two nests are slightly higher in elevation.

DATA COLLECTION. —All three nests had multiple established collecting paths. For all three nests I chose one path based on which had the most activity. Measurements and collecting were taken one meter from the entrance to the nest on workers returning to the nest. Data were collected every half hour while observing. Every 30 minutes, I took ground and air temperature measurements. I took ground temperature measurements by placing the thermometer on the ground (in the sun if present) along the collecting path. I allowed temperature to stabilize for three minutes before recording. For air temperature I held the thermometer in the sun and allowed it to stabilize for three minutes. At a designated point along the ant's collecting path, I collected the first 20 workers carrying leaf fragments to pass. Additionally at this time, I counted how long it took 50 carrying workers to pass that same point (as a measure of productivity). Data were collected early in the morning and later in the afternoon (when temperatures drastically rise and fall) in an attempt to collect specimen and record productivity for the full range of temperatures experienced by the nest.

Finally, head measurements for the collected ants were taken using a caliper. Therefore, each 30-minute temperature and productivity measurement had 20 measured worker sizes to go along with it. These 20 measurements were averaged to give an average worker size associated with each temperature measurement.

RESULTS

GROUND TEMPERATURE EFFECT ON PRODUCTIVITY. —Regression analyses were run for all three nests. Ground temperature and air temperature were highly correlated; ground temperature was used as it is the most influential for ant activity. Nest one (Fig. 1) showed a negative trend, though it was not statistically significant (F=2.621, P=0.1191, df=24), there being a slight increase in productivity with an increase in temperature. Nest two (Fig. 2) shows no relationship between ground temperature and productivity (F=0.3306, P=0.5811, df=9). The relationship between ground temperature and productivity in nest three is marginally significant (F=4.7072, P=0.0582, df=10; Fig. 3) meaning that productivity increases as temperature increases.

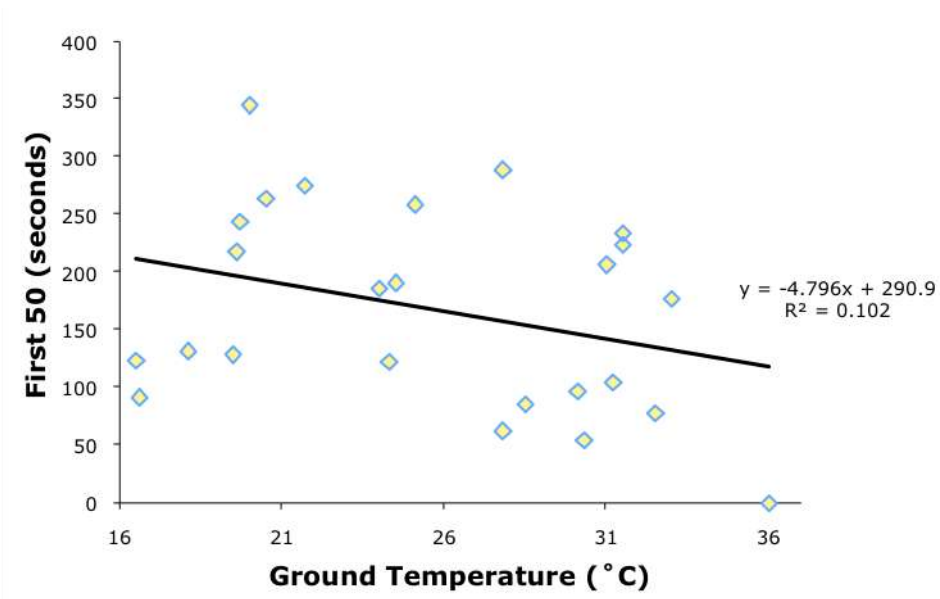

FIGURE 1. Relation between ground temperature and productivity (as measured by the time it took 50 *Atta cephalotes* ants to pass a designated point along collecting path) in nest one (Don Juan). (N=24). Regression was not significant (p > 0.05).

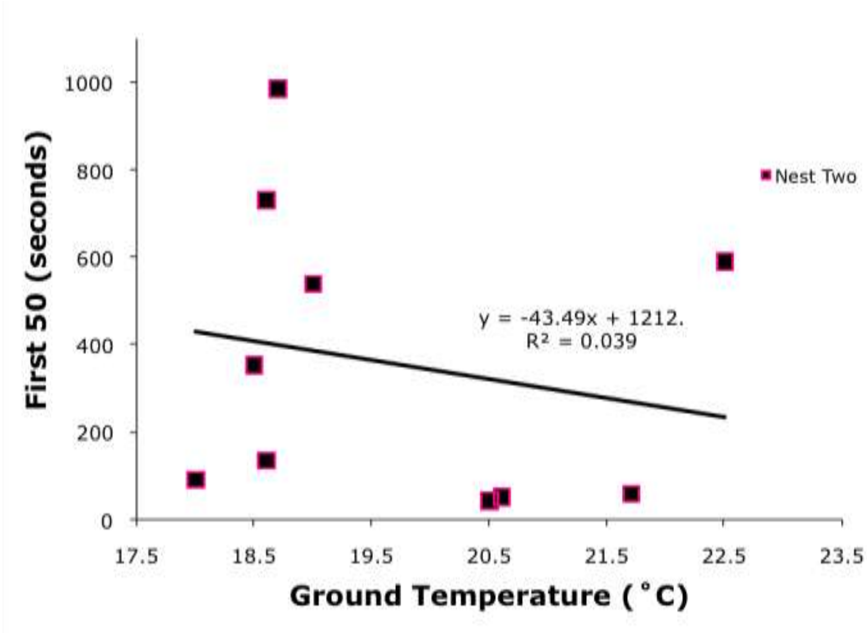

FIGURE 2. Relation between ground temperature and productivity (as measured by the time it took 50 *Atta cephalotes* ants to pass a designated point along collecting path) in nest two (Bajo del Tigre). (N=10). Regression was not significant ($p > 0.05$).

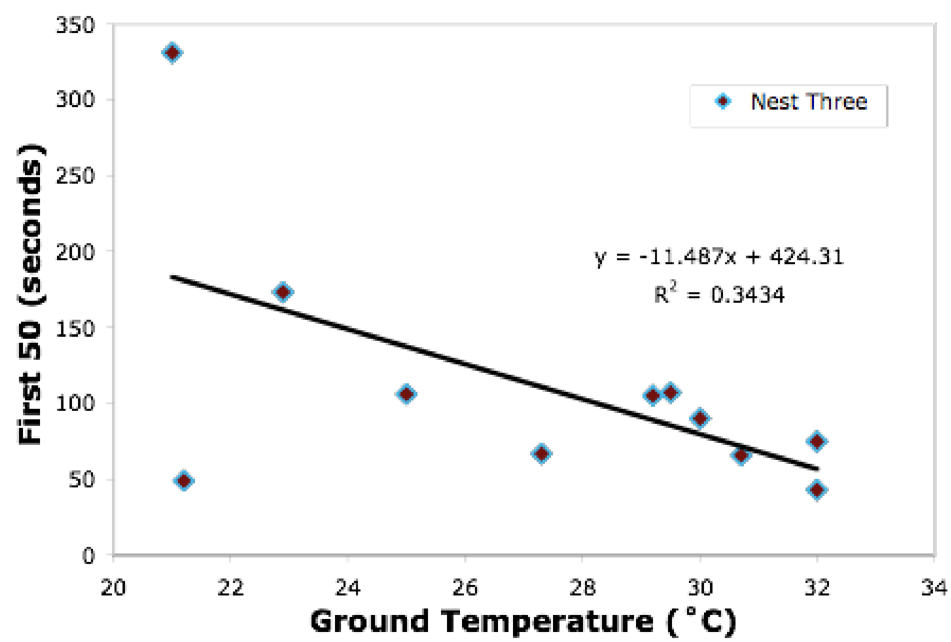

FIGURE 3. Relation between ground temperature and productivity (as measured by the time it took 50 *Atta cephalotes* ants to pass a designated point along collecting path) in nest three (open field in Cañitas). (N=11). Regression was marginally significant ($p = 0.058$).

WORKER SIZE DIFFERENCES BETWEEN NESTS. —It was found that there is a significant difference in average worker size between the nests ($F = 17.8716$, $df = 41$, $p < 0.0001$; Fig 4), nest one and nest two have significantly bigger ants than nest three. There are no significant differences between nest one and nest two.

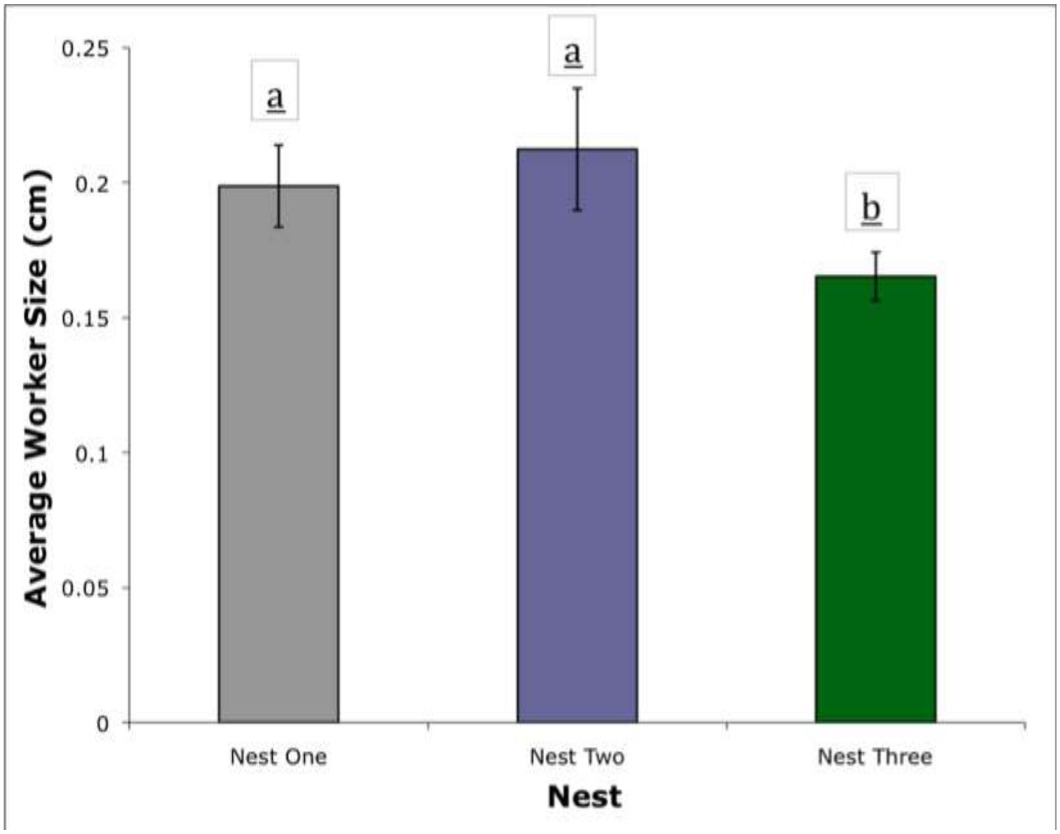

FIGURE 4. Average carrying worker size for each of the three *A. cephalotes* nests. An ANOVA was used to determine differences between nests, same letter above columns mean similar size of ants (Tukey test, $p > 0.05$).

EFFECT OF TEMPERATURE AND NEST ON WORKER SIZE. —Figure 5 plots the relationship between temperature and size of workers for all three nests on the same graph. I performed an analysis of covariance (ANCOVA) to evaluate how worker size related to ground temperature and nest. The ANCOVA model explained 68% of the variance in workers size ($F = 15.84$, $df = 42$, $p < .0001$). There is a significant effect of nest ($F = 18.19$, $df = 2$, $p < .0001$) and of ground temperature ($F = 12.12$, $df = 1$, $p = 0.0013$), including an interaction between the 2 variables ($F = 4.47$, $df = 2$, $p = 0.018$). This means that there were different responses towards increasing ground temperature between nests, as can be seen in Fig. 5. There was a bigger effect in nest two than in nests one and three.

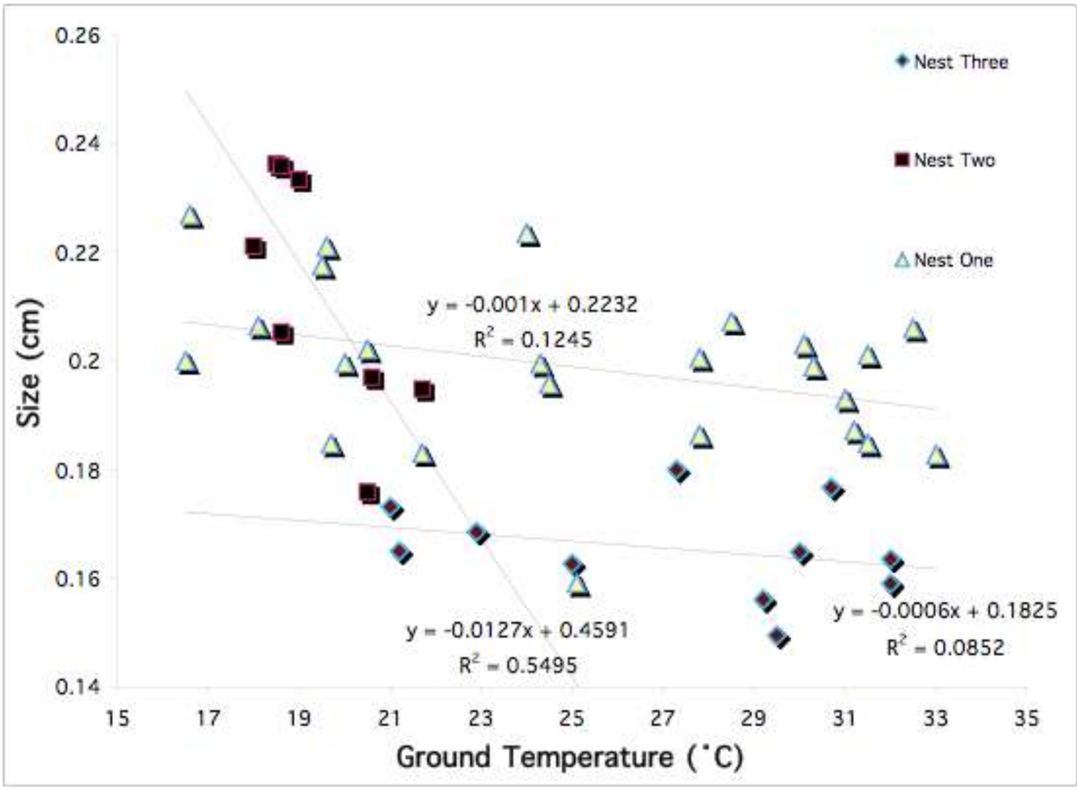

FIGURE 5. Ground temperature's effect on the size of carrying workers (measured by head sizes of collected workers) (N=43).

DISCUSSION

The inconsistent relationship between first 50 (productivity) and ground temperature in nests one, two, and three is probably due to differences between the nests. Differences in colony size, foraging rhythms, or microclimate location could be causing the nests to respond differently to variable thermal environments (Crist & Williams 1999). None of the nests were found to have a definitive minimum and maximum temperature when they either start or stop working, respectively (although for nest one there is a point when ground temperature reached 36^{o}C and the colony stopped working). For nest two, this can probably be explained by the fact that the colony only experiences a small range of temperatures because it is in the shade. Had there been larger fluctuations in temperature, the colony may have showed a response in productivity. Nest three is the youngest of the nests so the workers are the smallest. In 2007, Azcárate *et al.* found that worker speed (and thus productivity) had a higher positive correlation with temperature for smaller ants. This could explain the statistically significant relationship between temperature and productivity in nest three.

Nests one and two had, on average, bigger workers size than nest three. This can be explained by the relationship between colony age and worker size. Older colonies have larger workers (Wilson 1983).

The trend that arises Figure 5 is particularly interesting. Plotted independently, only nest two shows a significant decrease of size with increasing temperature though nest one shows the same trend. Nest three simply does not have the same size range of workers that the other two nests have. So, sending out larger workers is not even an option—small workers have to be working all the time because there are only small workers in the nest. It does seem that the smaller workers in nest three start working at warmer temperatures. Nests one and two have larger workers working around 18 ˚C while nest three does not start working until around 21 ˚C.

The overall trend is only appreciated when all data is considered together, it may be that the full range of worker size (which can only be modeled if all three nests are together) is needed to see the interaction. This model shows us again that there are significant differences between nests that explain much of the variation. Crist and Williams (1999) found that ant response to soil temperature may be affected by topographic variability, the amount of plant cover on or around the nests, or natural shifts in foraging rhythms. All of these factors are certainly different between the three nests.

All three nests are acting differently. This implies that sweeping hypotheses and predictions about *Atta cephalotes* must consider differences between every nest. But the study did also show that ground temperature affects productivity and size at least for some nests. This conclusion is interesting and implies some limits and activation factors for a keystone species in tropical ecosystems.

ACKNOWLEDGMENTS

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