

SHORT COMMUNICATION

A thermophile in the shade: light-directed nest relocation in the Costa Rican ant *Ectatomma ruidum*

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In tropical climates, nest movements by mature ant colonies are probably widespread but the phenomenon of nest relocation is poorly described (McGlynn 2007, McGlynn *et al.* 2004, Smallwood 1982a). For species that nest in soil, the costs and risks associated with excavating and establishing new nests are consequential, and it is assumed that relocation occurs when the costs are offset by a more advantageous nest location (Averages-Weber & Monnin 2009, Banschbach & Herbers 1999). Nest movements may occur to areas with greater availability of food resources or to a more favourable microclimate. Here we provide the first report of nest relocation in one of the most widespread and well described ant species in the Neotropics, *Ectatomma ruidum* (Roger), and we perform a manipulative experiment to test whether food availability or light environment influence nest movement.

The ant *Ectatomma ruidum* is a dominant feature of tropical wet and moist forests throughout the Neotropics. Colonies of *E. ruidum* nest in exceptionally high densities, and it is well established that the species is thermophilous on the local scale, as unshaded areas support much higher colony densities than adjacent shaded areas (Lachaud 1990, Santamaria *et al.* 2009, Schatz & Lachaud 2008). In north-eastern Costa Rica, densities are at least 1 colony m⁻² and often much higher, though colonies are rarely found in old-growth forests with closed canopies. The pattern of shade provided by canopies of secondary

forests and partially cleared areas is stochastic (Nicotra *et al.* 1999), and nest movements of *E. ruidum* may be directed toward increasing insolation, as is the case with the temperate ants in the *Aphaenogaster rudis* complex (Smallwood 1982b). Anecdotal observations by the first author and another investigator (B. Guenard, pers. comm.) suggest that nest movements by *E. ruidum* may be directed towards increased food availability.

The foraging ecology and behaviour of *E. ruidum* are well described, and this knowledge is useful for interpreting the causes and consequences of nest movements. *Ectatomma ruidum* is a generalist forager and collects a diversity of arthropod prey and often forages on low vegetation collecting nectar and honeydew. *Ectatomma ruidum* individuals and colonies are highly attuned to the availability and acquisition of food. *Ectatomma ruidum* demonstrates the ability to remember the time and place of prior food-availability events, returning to specific locations or orientations at moments of predictable food availability (Franz & Wcislo 2003, Schatz & Lachaud 2008, Schatz *et al.* 1999). *Ectatomma ruidum* workers ambush sweat bees at their nest entrances (Schatz & Wcislo 1999) and colonies house specialized intraspecific thieves that remove high-quality food items after they enter the nests of adjacent colonies (Breed *et al.* 1999).

We hypothesize that nest movements by *E. ruidum* are carried out to increase insolation and access to food resources. To evaluate the relative import of microclimate and food access, we designed a factorial manipulation of food and light, with independent and overlapping treatments of food supplementation and artificial shading. We expect that shading will result in the emigration of

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E. ruidum colonies, and that the provision of supplemental food will diminish the effect of shade on emigration.

Work was conducted June–July 2009 in La Selva Biological Station, located in a tropical rain forest in north-eastern Costa Rica. More information about La Selva is available at www.ots.ac.cr. We created 17 sites in two locations with high densities of *E. ruidum*, both areas maintained with scant understorey cover which facilitated comprehensive location of all *E. ruidum* colonies. With respect to the La Selva trail system, one location was centred c. 50 m east of the Sendero Oriental at the 550-m mark, and the other was located along both sides of the Sendero Sura near the 500-m mark. Each site contained four plots located at least 3 m from one another, for a total of 68 plots. Each site was at least 5 m from all other sites. Each plot was 1 m² and a focal nest was located in the centre of the plot.

We measured the density of nests at the outset of the experiment with a careful search for nest entrances and foragers at times of high foraging activity, as well as the use of several baits m⁻². At least one person-hour m⁻² during peak time of active foraging was spent on each plot, and plot designation occurred haphazardly without respect to nest densities.

Four treatments were designated in equal frequencies, such that there was one plot per treatment per site: unmanipulated (control), shade, food, or shade + food. In the shade treatment, the plot was shaded for 21 d with a heavy shade cloth elevated 0.5 m above ground level and extending 0.5 m beyond around the perimeter of the plot, mounted on a frame of PVC tubing. Food supplementation plots received daily supplemental food for 21 d using resources that have attracted *E. ruidum* to baits in prior studies. A variety of foods were used, including peanut butter, sucrose solution, crumbled cookies and canned tuna, with one kind of food proffered each day. All four treatments were monitored on 7-d intervals to check for occupancy of focal nests and for the arrival of immigrant colonies, obvious from nest excavation activity within the previous 7 d. Shade + food plots received shade and food treatments simultaneously. Throughout the 21-d treatment period, three plots were excluded from the experiment because of anomalous events (including erosion from flooding) that would have interrupted normal nest movement patterns.

Statistical analyses were conducted with JMP 8.0.1 (SAS Institute, Cary, North Carolina, USA). To ensure comparability of treatments, initial nest densities of plots were compared using a Kruskal–Wallis test. We used a Generalized Linear Mixed Model (Bolker *et al.* 2009) to evaluate the effect of treatments and nest density on the number of nest movements.

Nest movements were inferred when a new nest was detected after plot establishment in a plot in which we had previously exhaustively searched, with evidence of fresh

Table 1. Results from a Generalized Linear Mixed Model evaluating the effect of food, shade, nest density and an interaction between food and shade on the number of immigrant nests into treatment plots.

Source	df	χ^2	P
Whole model	4	13.6	0.0085
Food	1	0.0002	0.987
Shade	1	10.1	0.0015
Nest density	1	1.06	0.304
Food × Shade	1	0.230	0.632

excavation activity. Nest movements were not directly observed, even though we spent substantial time in the research plots. We suggest that relocation events occurred rapidly or that they only occurred under the cover of darkness when we did not work in the plots; the latter is likely in the gypsy ant *Aphaenogaster araneoides* (McGlynn 2007).

Mean initial nest density was 1.96 nests m⁻². There were no significant differences among the four treatment categories at the outset of the experiment ($\chi^2 = 4.57$, $df = 3$, $P = 0.22$). Contrary to our predictions, no focal nest (nor any other nests inside the plots to our knowledge) emigrated from any of the control and treatment plots. However, there were a number of immigrations into the plots from colonies outside the treatment plots, which were non-randomly distributed among treatments.

A search of the plots revealed a total of 26 immigrant nests in the plots 2 wk after commencement of treatment, with the following distribution: control: 4; food: 4; shade: 9; food + shade: 9. Of these immigration events, only the shade and shade + food plots received multiple immigrant event colonies, with three colonies moving into one of the shade plots, and two colonies moving into two of the shade plots, two colonies into three of the shade + food plots. The GLMM (Table 1) indicated a positive effect of shade on colony immigration, but not an effect of food, initial nest density, or a shade × food interaction.

We were surprised to find that colonies overwhelmingly moved under the artificial shade. Colonies preferentially preferred the shade treatment in the open area to adjacent naturally shaded areas. We infer that the high density of *E. ruidum* in open areas is not caused by a preference for high light levels as a preferred microclimate. One potential though unlikely explanation for higher densities of *E. ruidum* in sunny areas is that the shaded plots may have provided higher availabilities of food, including insect prey, nectar and honeydew. The diet of *E. ruidum* is rich in carbohydrates by choice (Cook & Davidson 2006) and there was an appreciable quantity of carbohydrate available in our supplemental food. We are partial to other possible explanations, as our manipulation of food supports the hypothesis that the relocation behaviour is independent of food availability.

What are the characteristics of open habitats that facilitate high nest densities even though *E. ruidum* prefers to nest in shade? Classic ant ecologists will be quick to suggest competitive exclusion from shaded areas (Hölldobler & Wilson 1990). The foraging strategy of *E. ruidum* features opportunistic food collection and agonistic interactions are avoided (McGlynn & Kirksey 2000). In a temperate forest, ants with a broader range of thermal tolerances are competitively subordinate to those with narrow thermal ranges (Lessard *et al.* 2009). However, *E. ruidum* is known to occur at very high densities alongside many other species, even in shaded old-growth environments (Levings & Franks 1982). Relative to other species in Neotropical forests, *E. ruidum* has a broad tolerance for light conditions, as the species ranges from southern Mexico to Amazonia (Kugler & Brown 1982). Rather than moving into the shade treatments out of constraint, we suspect that nest movements occurred to optimize nesting conditions. One working hypothesis is that shaded environments are preferred over sunny environments, and that higher nest densities in the sun are the consequence of smaller colony sizes in sunny environments as a result of thermal stress that can reduce foraging opportunities.

The creation of a shade apparatus in a sunny clearing does not provide an environment equivalent to that provided by the long-term shade of a tree. The nests of *E. ruidum* in sunny and shaded areas in our site was presumably at equilibrium because nest movements are otherwise apparently rare. We altered this equilibrium by providing an immediate shade opportunity that was distinct from established shade and sun regimes.

The present study provides a note of caution against broad applications of macro-ecological theories to single species on the local scale. Macro-ecologists disagree whether the large-scale patterns in ant diversity are structured by resources, or by temperature limiting resource access (Kaspary *et al.* 2004, Sanders *et al.* 2007). This question cannot be wholly answered by any single approach or at the scale of the present study. Nevertheless, the present results suggest that the interaction between trophic ecology and behavioural ecology complicates community assembly. Observed patterns in the abundance and distribution of species with respect to productivity and energy access do not necessarily inform predictions at the level of individual species. We conclude that competitive asymmetries, niche breadth and complexities in foraging behaviour must inform predictions of occupancy and density.

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