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Natural History Observations on the Velvety Tree Ant (*Liometopum occidentale*): Unicoloniality and Mating Flights

by

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ABSTRACT

The velvety tree ant (*Liometopum occidentale* Emery) is a dominant ant species found in Californian pine and oak woodlands. We performed a series of experiments to examine the degree of intraspecific aggression between nests. Within a site locality, ants collected from distances over a kilometer apart showed no aggression. However, ants from separate sites (more than 150 km apart) were strongly aggressive towards each other. Observation of food collection from baits further showed that *L. occidentale* trails can exceed over 70m. These combined observations suggest that *L. occidentale* has a natural life history that exhibits unicoloniality with perhaps the formation of large, habitat-dominating supercolonies. We also report an observation of a mating flight of *L. occidentale* that suggests females do disperse from their natal nests.

INTRODUCTION

The velvety tree ant (*Liometopum occidentale* Emery) is one of the most common and dominant ants in the oak and pine forests of Southern California (Wheeler & Wheeler 1986; Ward 2005). It is an occasional pest that invades houses (Gulmahamad 1995), but it has been little studied in the field since the original work of Wheeler (1905) and Shapley (1920, 1924). Colony trails are maintained for long intervals of time, with many not changing for years. Ants run along these trails mostly unburdened, apparently patrolling (Shapley 1920). *L. occidentale* is known to be opportunist omnivore (Wheeler 1905). Although the species can be active day or night, the speed of the ants is a function of the temperature, so that activity is highest between noon and

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evening (Shapley 1920, 1924). Colonies are apparently very large given the number of ants observed on trails and the length of the trails. Wheeler (1905) often observed columns of ants disappearing under rocks, but never found the nest or any brood under the rocks. The nest itself was likely located deep under large boulders or within the roots of large trees.

The goal of this study was to determine area size of single colonies of *L. occidentale*. The methodology included tracking the dispersion of provided food items, and measuring aggression between workers collected from various distances apart. The results strongly suggest that *L. occidentale* exhibits no intraspecific aggression over wide geographic areas and, therefore, has a unicolonial social structure. In conjunction with our experiments, we observed a mating flight of this species and report on those details.

METHODS AND RESULTS: COLONY AREA AND INTERACTIONS

The study took place in forested areas in the University of California's James Reserve in the San Jacinto Mountains (33 48' N, 116 46'W) and Stunt Ranch in the Santa Monica Mountains (34 6' N, 118 39' W). The two locations are separated by ~150 km. At each location, we identified several sites where *L. occidentale* were present on a regular basis. We used 15 sites in the James Reserve and 3 sites in Stunt Ranch. The sites in James Reserve were located on hiking trails and were between 100 to 1100 m apart. The sites at Stunt Ranch were in a single transect, with 100 m between collection sites. The forest canopy at the James is dominated by Jeffrey and sugar pines (*Pinus jeffreyi* and *P. lambertiana*) and black and canyon oaks (*Quercus kelloggi* and *Q. chryaolepis*), while the dominant vegetation at Stunt is coast live-oak (*Q. agrifolia*) and chaparral (*Garrya congdonii*).

Foraging experiment

We placed food (Pepperidge Farm Goldfish® Colors crackers) near established trunk trails of *L. occidentale* at the James Reserve site. These crackers were chosen because their colors contrasted with the ants and surrounding foliage, providing us a way to trace movement of the bait. To track multiple bait sites within one colony, we used the four different color crackers available: orange, green, purple, and pink. Located 20 cm away from the trunk trail, the bait site contained 3 crushed Goldfish® distributed evenly through a 5 x 5 cm area. To better follow *L. occidentale* trails we cleared one 30 m by 50 m section of the forest around one ant-containing oak tree. We added crackers of different color at different locations in the cleared area. We repeated this experiment in two other locations containing large trails of *L. occidentale*, but did not clear the area of debris. For several days afterward, we checked the area and attempted to follow the colored crumbs back to a nest. If necessary, we removed rocks and dead logs that obstructed our view of the trail.

The clearing of the forest floor allowed us to closely follow ants, and it was quickly observed that the trails went far past the boundaries of the 30 x 50 m area. The different colors of crackers demonstrated that ants moved crumbs great distances. In one case, an ant was observed with a crumb from a bait site over 70 m away. Travel along trunk trails was often erratic, with ants carrying crumbs one direction, only to turn around after some distance and carry it the other direction. Such behavior was observed for several hours without any apparent progress towards a central nest. Following crumbs sometimes led to rocks and dead logs in which the worker with the food disappeared and did not appear. After removing the obstruction, hundreds of workers would be discovered underneath; occasionally, a cache of resources was also found there, including conspicuous piles of colored crackers.

Aggression experiment

To test aggression, we placed 5 ants from one site against 5 ants from another together in a petri dish and allowed the trial to continue until an accurate aggression reading could be attained (a minimum of 5 minutes). Ants that needed to be transported to the test site were provided honey water and kept at ambient temperature in the shade. Besides intraspecific tests, we measured aggression between *L. occidentale* and six other species of ants (*Camponotus vicinus, Myrmecocystus ewarti, M. testaceus, Pogonomyrmex subnitidus, Solenopsis maniosa* and *Tapinoma sessile*). Each pairwise comparison was replicated four times, and the mean value was used for comparison. The same procedure was used for both interspecific and intraspecific aggression tests.

In order to get consistent scores we categorized aggression relative to the length of fighting, number of ants participating, injured/dead ants, and type of aggressive behaviors, on a 0 to 5 scale. The aggressive behaviors included leg biting and pulling, lock and rolls (two ants locked mandibles and balled up into an aggressive encounter), and open mandibles (a good indicator of preparedness for aggression). The scale is as follows:

0 – No aggression: antennation and ignoring were the only forms of behavior exhibited.

1 – Low aggression: Very short scuffles of leg biting/pulling (<5s). No lock and rolls. Mandibles sometimes open, but usually closed. No more than two ants fight.

2 – Medium low aggression: Short scuffles of leg biting/pulling (<10s). Very short, if any, lock and rolls (<4s). Mandibles open slightly less often than they remain closed. Less than half the ants fight.

3 – Medium aggression: Scuffles of leg biting/pulling frequently last longer than 10s. Lock and rolls occur and may last longer than 20s. Mandibles open more frequently than closed. Most ants participate in fighting.

4 – Medium high aggression: Continuous fighting of all sorts, but not necessarily by all ants. Mandibles almost always open. Injuries and some dead ants result.

5 – High aggression: Continuous fighting of all or almost all the ants. Mandibles are almost always open. Many injured and dead ants result by the end of a trial. Any score of 3 or higher strongly suggested ants treated each other as non-nestmates.

Workers of *L. occidentale* were highly aggressive towards all other species (Mean aggression scores > 3). However, *L. occidentale* workers showed no intraspecific aggression within locality (Mean aggression scores < 2 for all sets of 4 replicates, for all 15 pairwise comparisons at James and 3 pairwise comparisons at Stunt). The three Stunt sites were tested against three comparative sites from James (#s 1, 10 and 14). Significantly greater aggression occurred between *L. occidentale* workers from different localities relative to within-locality interactions (unpaired t-tests, $p < 0.001$ compared to James; $p = 0.007$ versus Stunt). Aggression, however, was not completely uniform across all presentations. Stunt 1 and 3 were aggressive to all three James sites (Mean scores > 3), but Stunt 2 was aggressive to James 1 and 10, and not James 14 (Mean score < 2). Overall, the results indicate that *L. occidentale* workers are not universally accepting of each other.

METHODS AND RESULTS: MATING FLIGHT

A large aggregation of *L. occidentale* winged female and male sexuals was observed at a large standing dead sugar pine tree (*P. lambertiana*) at 0940 on May 20, 2007 in the James Reserve (33° 48' 30" N, 116° 46' 40" W). The dead tree was at the top of the Four Saints trail (elevation 1840 meters). The morning was warm with no winds.

The alates climbed rapidly to the top of the tree. Large numbers of very active and aggressive workers swarmed across the tree and on ground surrounding the tree. Many of the alates did not fly away, but eventually retreated back down the tree. By afternoon, no more alates were observed in the area. This nest was checked thereafter every day from May 20-24, but no resumption of flight activity was observed (even though weather conditions were similar). This location had been visited during the previous week but no obvious activity had been observed. During the whole time period of the experiments (May 14-24), no other flight activity was observed in the James Reserve although *L. occidentale* workers were highly active in foraging throughout the period. A May mating flight is consistent with previous information on this species (Del Toro *et al.* 2009).

DISCUSSION

Our results suggest that there is nestmate recognition between colonies of *L. occidentale*. However, the lack of aggression between workers from sites more than a kilometer apart also strongly suggests unicoloniality in colony organization within any locality. The lack of aggression paired with sprawling foraging trails over 60 meters long also makes it highly unlikely that there is one central nest with one or several queens producing square kilometers worth of *L. occidentale* workers. Our observations suggest that colony size in this species may be far larger than the previous estimates of 60,000 workers (Del Toro *et al.* 2009).

A very interesting result is that some sites separated by more than 100 km are not aggressive to each other. There are two possibilities that may account for this variance in aggression. One is they still share similar genetic markers. This would suggest that there may be relatively few 'recognition' alleles that distinguish colony members throughout the range of this species. A similar mechanism is proposed for variation in aggression within and across two

Pheidole species (Langen *et al.* 2000; Tripet *et al.* 2006). The other possibility is that recognition is predominantly determined through environmental cues that are all locally shared. Hence ants in a predominantly pine forest (the James) would mostly, but not always, have different cues than ants from an oak forest (Stunt). Environmental cues as the source for discrimination and aggression have been demonstrated in the generally unicolonial Argentine ant (Chen & Nonacs 2000; Silverman & Liang 2001).

The intraspecific aggression patterns in *L. occidentale* are interesting to compare to the best studied unicolonial species, the Argentine ant, *Linepithema humile*. A unicolonial life history may improve the discovery, defense and retrieval of food, and thus allow such species to dominate large habitat ranges and other species of ants (Holway 1999; Holway & Case 2001). Thus, dominance of *L. humile* over native species across the globe (Cole *et al.* 1992; Holway 1995; Giraud *et al.* 2002) has largely been attributed to the lack of intraspecific aggression in the introduced population (Holway 1998). Certainly *L. occidentale* appears to be the most dominant native ant species in the habitats that it is found, and this may also be due to a shared predilection for unicoloniality.

Unicolonial species tend to saturate their environments as supercolonies, where each colony may have an exclusive, defended territory that can be as large as thousands of square kilometers and contain millions of individuals (Helantera *et al.* 2009). In their native habitat, Argentine ant supercolonies appear to range in size from 1-515 m as determined by linear transect (Vogel *et al.* 2009). We could not determine the extent of unicoloniality in our populations of *L. occidentale* because we never found boundaries within our two localities. Future studies will be required to determine the geography and distribution of supercolonies in *L. occidentale*.

There is one clear difference in the life histories of velvety tree ants and Argentine ants. Our observation of mating flight behavior suggests that *L. occidentale* mates outside of the nest. Although it is unknown whether mated females start their own colonies or return to their natal nest, mating outside of the nest would create gene flow between adjoining supercolonies through male dispersal. In contrast, Argentine ants apparently always mate within their natal nests and there is no gene flow even between adjoining supercolonies (Vogel *et al.* 2009). Determining the genetic structure of *L.*

occidentale populations is a very obvious next step for understanding this species' social biology.

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