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REVIEW

A Review of the Biology, Ecology and Behavior of Velvety Tree Ants of North America

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Abstract

Ants belonging to the genus *Liometopum* are regionally distributed across North America, Europe and Asia. *L. apiculatum* Mayr, *L. luctuosum* Wheeler, and *L. occidentale* Emery are found in western North America and are referred to as velvety tree ants. Very little is known about the biology of these species, but they are similar. They are typically associated with trees and shrubs and are frequently found tending hemipterans. All three species are easily disturbed and resort to highly aggressive behaviors including the use of strong alarm odors. The following review is intended to summarize the literature regarding the biology and control of these species. Special emphasis has been given to factors that might be important in their control and gaps in our current knowledge.

Introduction

The genus *Liometopum* consists of 9 fossil and 8 extant species scattered over North America, Europe and Asia (www.antcat.org/catalog/329538). There are three North American species, found in the western U.S. and Mexico: *L. apiculatum* Mayr, *L. luctuosum* Wheeler, and *L. occidentale* Emery. The genus *Liometopum* belongs to the subfamily Dolichoderinae, which also includes other important structural pest ants such as the Argentine ant, *Linepithema humile* (Mayr), and the odorous house ant, *Tapinoma sessile* Say. According to Del Toro et al. (2009), *Liometopum* is only a “minor pest in and around rural housing areas” and “no severe damages to housing or property have been reported,” although the “uncomfortable bite and smell of this ant makes it a nuisance to affected residents.” However, structural damage has been reported for two species, *L. luctuosum* and *L. occidentale* (Wheeler & Wheeler, 1986; Merickel & Clark, 1994; Gulmahamad, 1995; Hedges, 1998; Klotz et al., 2008). Homeowners commonly complain of the odor associated with an infestation of velvety tree ants.

L. luctuosum and *L. occidentale* are often mistaken for carpenter ants (*Camponotus* spp.) by homeowners and Pest Management Professionals (PMPs). This mistaken identity is due to morphological and behavioral characteristics they share with carpenter ants; namely polymorphic workers, a smooth convex thoracic profile, and the tendency to excavate wood (Klotz et al., 2008). *L. luctuosum* are also often confused with the *T. sessile* since they have the same coloration, are similar in size, and produce an alarm pheromone with a very similar odor. Consequently, their importance as structural pests may be greatly under reported, especially in California, Oregon, and Washington.

All three North American species are easily disturbed and when aggravated, they resort to highly aggressive defensive behaviors, biting and releasing strong alarm odors from their anal glands (Del Toro et al., 2009). They produce a noxious alarm pheromone (described as smelling like rotten coconut or having an intense butyric acid-like odor). This pheromone consists of 6-methyl-5-hepten-2-one, acetic acid, n-butyric acid, and 3-methylbutyric acid (isovaleric acid) (Casnati et al., 1964). Alarm pheromones

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of many dolichoderines seem to be less species-specific than olfactory sex attractants and other pheromones. For instance, the alarm pheromones of *Forelius pruinosus* (Roger), *Dolichoderus bispinosa* (Olivier), *L. occidentale*, and T. sessile will mutually affect one another. In *L. occidentale* this pheromone originates in the anal gland (Wilson & Pavan, 1959).

In Mexico, colonies of *Liometopum* have been used as a food resource by people in rural areas for centuries. The immature stages of the reproductive caste, known as "escamoles" are consumed and are a high-quality source of protein, carbohydrates, and lipids. Adult reproductives may also be consumed by humans during swarming, and worker brood is consumed when other stages are scarce (Ramos-Elorduy & Levieux, 1992). Consequently, considerably more is known about the biology of *L. apiculatum* than any of the other species.

Taxonomy

Liometopum occidentale was originally described as *Liometopum microcephalum* var. *occidentale* by Emery (1895). Wheeler (1905) relocated it to a variety of *Liometopum apiculatum*. It was finally elevated to the species level by Wheeler (1917) and remained there in a recent taxonomic review by Del Toro et al. (2009).

Liometopum luctuosum was originally named *Liometopum apiculatum* subsp. *luctuosum* by Wheeler (1905) and Forel (1914). Creighton (1950) relocated it to a subspecies of *Liometopum occidentale*. It was elevated to the species level by Wheeler & Wheeler (1986), and subsequently confirmed by Mackay et al. (1988) and Del Toro et al. (2009).

Liometopum apiculatum was first described by Mayr (1870), who described the workers of this species. Emery (1895) later described the queens of this species; Wheeler (1905) described the males and Wheeler & Wheeler (1951) described the larvae. Shattuck (1994) considered *L. apiculatum* a senior synonym of *Liometopum masonium*. This species was also confirmed by Del Toro et al. (2009).

Caution should be exercised when examining the literature prior to the review by Wheeler and Wheeler (1986) in regards to *L. luctuosum*. However, *L. luctuosum* has only been reported in the southwestern U.S. and not Mexico. Workers of *L. luctuosum* are significantly smaller (n = 38, 0.91 - 3.53 mg) than *L. occidentale* (n=40, 1.44 - 5.24 mg).

Habitat/distribution

Liometopum apiculatum ants are found in arid and semi-arid regions of southwestern U.S. and Mexico to Quintana Roo (Del Toro et al., 2009). They extend from Colorado through Texas, New Mexico, southeastern Arizona, and south into Mexico (Gulmahamad, 1995). They are usually found at elevations between 1000 and 2500 m, but their prime habitat is oak forests found around 2000 m. At higher elevations they are found in pinyon pine zones, up to the ponderosa pine and riparian zones; at lower elevations they inhabit creosote bush scrub and grasslands in microhabitats of clay, under rocks, boulders, and decaying logs (Del Toro et al., 2009). They have also been found in foothill meadows, deciduous canyon forests, pinyon-cedar woodlands, ponderosa pine-cedar-oak woodlands, and cottonwood-willow forests (Mackay & Mackay, 2002). At high elevations, their abundance decreases and they are replaced by *L. luctuosum* (Del Toro et al., 2009). Altitude may play an important role in the distribution of *Liometopum*. In regions of Mexico explored by Conconi et al. (1983b), *L. luctuosum* and *L. apiculatum* are only found between 2000 and 3000 m. Although conditions below 1800 m looked favorable, they are absent. In the U.S., *L. apiculatum* is found from 1316 to 2438 m.

Liometopum luctuosum has been reported at elevations as low as 59 m (Dr. Laurel Hansen, Spokane Community College, personal communication, Sept. 6, 2012), but is typically found at elevations higher than 2400 m in more southern latitudes (Wheeler & Wheeler, 1986; Del Toro et al., 2009). The range of elevation of this species by state is as follows: WA: 59-724m, ID: 664-786m, OR: 277-454m, CA: 1280-1596m, and NV: 1372-2469m (Dr. Laurel Hansen personal communication, Sept. 6, 2012, personal collection) and above 2000 m in New Mexico (Mackay & MacKay, 2002). Their range extends from temperate habitats as far north as British Columbia (Canada), and to more arid habitats of Central Mexico and western Texas. They inhabit pine, oak, Douglas fir, and juniper forests, sagebrush, and high-elevation riparian habitats (Conconi et al., 1987a; Clark & Blom, 2007). This species is often strongly associated with but not limited to pine trees (Del Toro et al., 2009).

Liometopum occidentale is found from sea level to over 1840 m in coastal regions from southern Washington to northern Mexico (Snelling & George, 1979; Del Toro et al., 2009; Wang et al. 2010; Dr. Laurel Hansen, personal communication, Sept. 6, 2012). The range of elevation of this species also appears to depend on latitude with ants collected from locations in Oregon as low as 7 m and up to 1700 m in California (WA: 31-142m, OR: 7-348m, CA: 142-1713m; Dr. Laurel Hansen, personal communication, Sept. 6, 2012, personal collection). They are the most common and dominant ant in oak and pine forests of southwestern U.S. (Wheeler & Wheeler, 1986; Ward, 2005; Del Toro et al., 2009). They prefer to nest in the crevices of oaks, alders, elms, cottonwoods, and creosote, in soil, underneath bark of dead trees, and under rotten logs (Cook, 1953). Cook may be in error claiming that these are nests since we often see many, many adult workers in 'resting places' which are mistaken as nests, as noted by Klotz et al. (2008).

Within their distribution range, the elevations at which *Liometopum* are found decreases the further north the location. To definitively demonstrate that there is an effect of latitude on the elevation at which *Liometopum* is distributed in North America, a larger collection of these ants must be made.

Nests

Nests of *L. apiculatum* are typically located underground and have a very distinctive structure. They fill hollowed-out chambers with a branched network of carton-like material made out of agglomerated soil and oral secretions until the entire nest resembles Swiss cheese. Within the nest as many as 3 or 4 large chambers containing this honeycombed carton-like material can be found. The carton-like material of this species is much finer than that of *L. luctuosum*. *L. apiculatum* tend to nest at higher densities than do *L. luctuosum* (Conconi et al., 1987a). These ants are usually found nesting in dead logs, under stones, or in decaying stalks of *Yucca* spp. (Miller, 2007). They have also been collected in glass containers and rubber tires (Del Toro et al., 2009) and among the roots of various perennial xerophytes such as *Agave* spp., *Opuntia* spp., *Myrtillocactus geometrizans* Console, *Yucca filifera* Chabaud, *Senecio praecox* DC., *Schinus molle* L. or *Prosopis juliflora* DC. (Conconi et al., 1983b). In some habitats, the nests are deep under heavy boulders or large trees (Wheeler, 1905; Gregg, 1963a). The queen is always well protected and is usually in a remote place about 6-8 m from the largest chamber where the brood is stored. The chambers are connected by various galleries.

Liometopum luctuosum nest under rocks, decaying logs or at the base of large trees, or among the roots of trees such as *Quercus* spp., *Juniperus* spp. and *Pinus* spp. (Conconi et al., 1983b). They create carton nests similar in structure to *L. apiculatum* (Del Toro et al., 2009). Similarly, the queen of *L. luctuosum* is well protected at a remote place about 6-8 m from the largest chamber where the brood is stored, and the chambers of the nest are connected by various galleries (Conconi et al., 1987a).

Liometopum occidentale typically nest in soil, crevices of trees, and under the bark of dead trees (Del Toro et al., 2009). However, were never found by Wang et al. (2010) leading to the speculation nests must lie deep under large boulders or among roots of large trees. To better understand the structure of their nests, more nests need to be excavated.

Colonies

Colonies of *L. apiculatum* are polydomous with segments of nests (or satellite colonies) scattered over the landscape (Del Toro et al., 2009). Colonies are variable in size, ranging from a few hundred to hundreds of thousands of workers (Gregg, 1963b; Ramos-Elorduy & Levieux, 1992). Colonies exploited for their brood by humans contain between 65,000 and 85,000 individuals, while undisturbed colonies may contain as many as 250,000 individuals. Colonies remain useful for repeated brood collection by humans for 4 to 12 years (Ramos-Elorduy & Levieux, 1992).

Colony foundation in *L. apiculatum* is by haplometrosis (non-cooperative), that is, a single fertile queen founds each colony (Conconi et al., 1987a,b). Colony foundation behavior is not uniform among founding queens. The time spent exploring, excavating, and removing excavated materials and waste are usually higher throughout the day, while oviposition, brood care, and inactivity increase at night (Conconi et al., 1987b). Founding queens prefer sites close to bodies of water; however, sites slightly further from water are more conducive to the establishment of a successful colony as persistently high humidity will result in the early death of a colony due to fungal invasion (Conconi et al., 1983a).

Colony foundation in *L. luctuosum* is by pleometrosis (cooperative), in which 2 to 40 fertile queens found a single colony (Conconi et al., 1987a). Most colony foundation activities take place at night (Conconi et al., 1987b). There is a division of labor among founder queens. However, this is not always divided the same for each foundation event. The amount of time dedicated to each activity by each queen varies with each colony foundation event. Some queens are active in a variety of tasks. For example, some queens dedicate more time to brood care and others more time patrolling the nest area. The fewer ants founding together (3 or less), the more time spent per individual caring for brood, ovipositing, and exploring. Trophallaxis, patrol activity, and inactivity decreases in these cases, but brood care still remains the primary activity of founding queens (Conconi et al., 1987b).

After finding no aggression between workers collected from significant distances apart and no territorial boundary, Wang et al. (2010) speculated that *L. occidentale* colonies are large and polydomous. Since they never found brood or queens, it is uncertain whether there are multiple queens within a nest, or whether each queen has some localized "sphere of exclusivity." and it just seems unlikely that there could be just one queen that produces enough eggs to establish a colony that is one kilometer wide, they also speculated that *L. occidentale* are polygyne. Colonies have been estimated to contain between 40,000 and 60,000 workers (Ramos-Elorduy & Levieux, 1992; Del Toro et al., 2009). Colony foundation of this species has not been studied as well as it has with the other two North American species.

Feeding

Liometopum apiculatum are opportunistic carnivores and granivores, and have also been observed foraging on dead insects, larger colonies being more predaceous (Shapley, 1920). *L. apiculatum* also feeds on crustaceans, annelids, mollusks, dead vertebrates, animal droppings, and extrafloral nectar (Velasco et al., 2007). These ants also obtain nectar or pollen from bear grass and substances from the outside of the ovaries of the flowers of century plants (*Agave scabra* Salm-Dyck and *A. chisosensis* C.H.Mull.) and Spanish dagger (*Yucca* spp.). Workers have been attracted to various foods used as baits including apple sauce, sausage, vegetable soup, sugar water, and cookies. *L. apiculatum* have also been observed soliciting honeydew from insects including membracids (*Vanduzea segmentata* (Fowler)), aphids, and other ants (*Pogonomyrmex barbatus* (Smith, F.), *Camponotus sayi* Emery, and *Solenopsis xyloni* McCook; Van Pelt, 1971). In some habitats the honeydew produced by hemipterans, *Cinara* spp., *Dysmicoccus brevipes* (Cockerell) and *Saissetia oleae* (Oliver), are the main energy sources (Velasco et al., 2007). In other words, hemipteran exudates make up the bulk of the diet of *L. apiculatum* (Conconi et al., 1983b). Their role in disrupting biological control has not been determined.

Liometopum occidentale are opportunistic omnivores (Wheeler, 1905) and can often be found tending hemipterans and carrying prey insects back to the nest (Gulmahamad, 1995). They readily attend hemipterans and are found in citrus groves, but their role in disrupting biological control has not been determined. Their feeding preferences need to be studied to enable the development of an effective bait for pest control purposes.

Liometopum luctuosum is also an omnivore and has been observed feeding on secretions from both plants and insects such as aphids, membracids and scales, as well as miscellaneous foods such as meat, eggs, fruit and bread (Conconi et al., 1987a).

Foraging Activity

Ants of the genus *Liometopum* lay down a trail pheromone that has an odor similar to butyric acid, but its chemical composition remains unknown. The source of trail pheromones in many species of Dolichoderines is the Pavan gland, a medioventral sac between the sixth and seventh abdominal sternites (Pavan, 1955; Billen, 1985). This gland may be the source of these pheromones in *Liometopum*. All the dolichoderine trail pheromones tested so far have proved to be highly species-specific (Wilson & Pavan, 1959).

Dolichoderine foragers travel along trials in a manner described by Shapley (1920) as "trail-running", which we have observed as travelling rapidly along defined trails. The number of ants on these trails is governed largely by food and the speed of the ants by meteorological conditions. Shapley (1920) noted that *Liometopum* activity patterns are equally diurnal and nocturnal. *L. apiculatum* and *L. occidentale* are active at wide range of temperatures (8°C - 38°C), humidity (5%-100%), wind, and light, but temperature is the most important factor affecting their activity. Even in winter after a few warm days these ants have been observed foraging within a few feet of snow banks (Shapley, 1920), an example of how imperative temperature is to foraging activity of these ants. *Liometopum* appear to run at a speed very near the maximum speed possible under prevailing conditions, except at low temperatures. For temperatures below 15ºC, in which the activity level of these ants is very low, activity can be temporarily increased by exciting the ants into battle or by the discovery of food (Shapley, 1920).

Foraging trails for *L. apiculatum* and *L. occidentale* are maintained over long intervals of time and even years (Shapley, 1920). Ants on these trails are for the most part unburdened with prey or objects, no matter if they are going toward or away from the nest. Shapley (1920) suggests they are just patrolling, however, what is equally as likely is that these workers are carrying large amounts of honeydew or other liquid foods within their crop.

Liometopum apiculatum forage from March to September (Mackay & Mackay, 2002). Workers forage almost exclusively on trails as wide as 2-3 cm on the soil surface, and when the temperature rises sharply at midday, they cease foraging and seek shelter under stones (Conconi et al., 1983b; Ramos-Elorduy & Levieux, 1992). The movement of this species is less erratic than *L. occidentale* at higher temperatures. An increase in temperature by 30°C changes the speed by 15 fold, increasing exponentially from 0.44 to 6.60 cm a second. There also appears to be little difference in the speed whether ants are moving towards or away from the nest, or between large and small workers during the summer months. However, after prolonged periods (two months or more) of low temperatures, the larger workers are faster than the small workers. Also within a range of 14º to 38ºC there appears to be little effect of temperature on the number of ants on trails. Maximal activity occurs between 12p.m. - 12a.m during the summer months in southern alpine habitats such as Mount Wilson, CA (Shapley, 1920). In natural environments, ants of this species forage in areas between 468 and 708 m^2 (x = 612 m^2); however, they only use between 16 to 30% of this area at any given time. The spatial distribution of the foraging areas for these species seems to be strongly correlated with the location of shrubs and trees infested by hemipterans (Ramos-Elorduy & Levieux, 1992).

Liometopum occidentale form massive foraging trails that extend 60 m or more from the nest (Gulmahamad, 1995; Eckert & Mallis, 1937), and can even be observed on hot days with temperatures between 24 and 38°C (Tremper, 1971). Ramos-Elorduy & Levieux, (1992) observed *L. occidentale* traveling mostly underground in very shallow galleries (1-2 cm deep), or in leaf litter, however, we have also observed massive above ground trails. According to Ramos-Elorduy and Levieux (1992), *L. occidentale* in natural environments forage an areas as large as 2,000 m^2, but they only utilize between 486 and 1198 m^2 (x = 740 m^2) of this area at any one time. This means that they are only using between 33 and 68% of this area, more than twice that of L. apiculatum.

To reach a food source, *L. luctuosum* establish trails sometimes more than 100 m long. The galleries of these trails often run under leaf litter (Conconi et al., 1983a,b). This protection could explain why these ants can be found trailing at almost any hour of the day (Conconi et al., 1983b).

PMPs have stated they have observed both *L. luctuosum* and *L. occidentale* foraging during the day in great numbers in the spring and early summer, but around midsummer they switch to night time foraging. However, this has not been scientifically proven.

Interspecific Interactions and Nest-mate Recognition

Liometopum are highly competitive, behaviorally dominant ants and play an ecologically similar role to the behaviorally dominant Australian dolichoderines, *Anonychomyrma*, *Papyrius* and *Froggattella* (Andersen, 1997). Ant communities often have a hierarchal order to them, with "submissive" ant species being more adaptable, and "territorial" species at the top of this hierarchy defending territories of varying sizes (Petráková & Schlaghamerský, 2011). Ants fight in the spring when food is scarce and also fight to renew trails after winter pauses in activity (Petráková & Schlaghamerský, 2011). The interactions between *Liometopum* spp. and native ants have been studied for *L. microcephalum* Panzer, an Old World species. *L. microcpephalum* is a behaviorally dominant ant species in Europe and Asia. This species builds nests several meters above ground in old living trees (especially oaks) and forage in other trees in the vicinity of the nest tree, similar to North American species of *Liometopum* (Petráková and Schlaghamerský, 2011). Some colonies are polydomous. These ants are very efficient hunters, but also tend aphids. *L. microcephalum* can be very aggressive toward other ant species, attacking by biting and spraying secretions that repels enemies, and initiating alarm behavior (Petráková & Schlaghamerský, 2011). Aggressive behavior occurs close to the nest, on trails, on trees, and occasionally at food resources. *L. microcephalum* takes advantage of worker cooperation during aggressive interactions, a strategy used by smaller ants (Petráková &Schlaghamerský, 2011). Aggressive intraspecific interactions are expected with all three North American species due to such similarity in ecology and behavior of this species.

In Tlaxco, Tlaxcala, Mexico, *L. apiculatum* was found to associate with fourteen species of Hemiptera, including seven species of aphids (two in the *Cinara* genus, *Anoecia cornicola* (Walsh), *Aphis lugentis* Williams, *Aphis solitaria* (McVicar Baker), *Aphis helianthi* Monell, and *Aphis* spp.), three species of scales (*Saissetia* spp., *S. olee* (Olivier), two species of Pseudococcidae including *Dysmicoccus brevipes* (Cockerell)); one species of Ortheziidae, and one species of Dactylopiidae (*Eriococcus* sp.) (Velasco et al., 2007). Yet another species of hemipteran they associate with are cochineal scales *Crassicoccus* spp. that live on oak trees.

Competition between the invasive *Linepithema humile* and *L. occidentale* has been documented (Ward, 1987; Holway, 1998; Sanders et al., 2003). However, *L. occidentale* rarely co-exists with *L. humile*, perhaps because they are habitat or resource specialists that are found in such a wide range of habitats as *L. humile* or because they are weak competitors against invasive species (Sanders et al., 2003). However, *L. occidentale* is the species of *Liometopum* most affected by *L. humile* due to its "taxonomic and ecological similarities to *Linepithema humile* in that "they are members of the same subfamily (Dolichoderinae) and they are dominant, opportunistic, epigaeic (lives or forages primarily above ground) ants, with propensities to establish dense foraging trails, to tend Hemiptera: Sternorrhyncha, to move nest sites readily, and to forage and tend hemipterans under the same ambient conditions throughout the summer months (Ward, 1987). " This abundance of similarities makes them likely to compete in areas of co-occurrence.

Wang et al. (2010) tested the nest mate recognition of a limited number of *L. occidentale* colonies in James Reserve and Stunt Ranch in southern California. Results of this study showed that ants from sites separated by a kilometer or less were not aggressive to one another, while colonies separated by more than 100 km were aggressive to each other; although not every colony was always aggressive to every other one, even when arising from disjunct populations. Wang et al. (2010) also test the aggression of *L. occidentale* toward other ant species, *Camponotus vicinus* Mayr, *Myrmecocystus ewarti* Snelling, *M. testaceus* Snelling, *Pogonomyrmex subnitidus* Emery, *Solenopsis xyloni* McCook and *Tapinoma sessile* Say, and found that they were highly aggressive towards all these species.

L. luctuosum "has been reported as being a competitor of *Camponotus* species in Idaho, since both of them compete for similar nesting sites" (Merickel & Clark, 1994). However, *L. luctuosum* is the least studied of all the North American *Liometopum* species.

Polymorphism

Polymorphism in *L. apiculatum* and *L. luctuosum* has been described as bimodal with diphasic allometry (Conconi et al., 1987a). Bimodal or biphasic allometry occurs when animals such as ants have structures that vary disproportionately with body size such as the heads and mandibles of soldiers and major and minor workers (Grimaldi & Engel, 2005). At some intermediate, boundary size, larger individuals have a disproportionately larger structure, but the structure is disproportionately small below this size (Grimaldi & Engel, 2005). The average live weight of the largest workers of *L. apiculatum* is about 3.24 mg and the average weight of the minor workers are half this, but the extremes of weight for majors and minors are probably in the ratio of four to one (Shapely, 1920). The polymorphism of *L. occidentale* has not been described.

Reproduction

Immature stages of reproductives have been found in *L. apiculatum* nests from May to August, whereas the rest of the year the brood is of the worker caste (Conconi et al., 1983a; Del Toro et al., 2009). Males and gynes have been collected outside the nest from June to August and queens (likely founding queens) have been collected in July and August under stones and other landscape features (Del Toro et al., 2009). Nuptial flights of this species occur during the day after a heavy rain during the months of April or May (Conconi et al., 1983a). Before a nuptial flight there is a great agitation of the workers, which leave the nest and run rapidly in a "zig-zag" fashion. The male and female alates leave the nest, but are less active. After a while the workers begin to bite the legs and wings of the alates, forcing them to climb the nearest plant. The workers continue to excite the alates with bites until they begin to beat their wings, and subsequently initiate flight one by one, not as a swarm. Mating takes place in the air, and mated males and females fall to earth together, often still attached (Conconi et al., 1983a). The life span of *L. apiculatum* queens is shorter than that of *L. luctuosum* queens (exact time difference not specified); however, their productivity (oviposition) is greater (Conconi et al., 1987a).

The annual productivity for an established colony (60 to 85,000 workers) of *L. apiculatum* is about 3-3.6 kg of brood per year (Ramos-Elorduy & Levieux, 1992). Oviposition by founding queens is large, however, only a small percentage reaches the adult stage of the F1 generation, partly because the smaller, "trophic" eggs are consumed as food. After laying her first batch of eggs, the queen delays laying more until the first eggs have developed into pupae. Once the first workers emerge, the queen discontinues laying trophic eggs, which lowers the total amount of eggs laid but increases the proportion of viable eggs. Eggs are laid all year round (Conconi et al., 1983a).

Some virgin queens of *L. apiculatum* emerge from the nest, remove their wings, and dig a nest without mating. They will lay eggs, care for them, and eat them to survive. However, they only care for more recently laid eggs that have not turned yellow or dried out (Conconi et al., 1983a).

Flights of *L. occidentale* reproductives have been observed throughout May (Del Toro et al., 2009). The annual productivity for a colony (40 to 60,000 workers) of this species is 2 to 2.8 kg of brood per year for 4-8 years (Ramos-Elorduy & Levieux, 1992). Workers housed without a queen will also lay unfertilized eggs that are eaten or develop into males.

Reproductives of *L. luctuosum* have been observed flying in June and July and can be collected the day after the flight in large bodies of water or using a blacklight trap (Del Toro et al., 2009).

The most productive colonies of *Liometopum* are those that are more substantially surrounded by vegetation which likely contains honeydew excreting hemipterans. However, *L. apiculatum* appears to be more productive than *L. occidentale* even though *L. apiculatum* forages in a much smaller territory (Ramos-Elorduy & Levieux, 1992).

The reproductive life cycles of *L. luctuosum* and *L. occidentale* need further investigation.

Life Cycle

A study by Conconi et al. (1983a) recorded the longevity of each of the reproductive castes and colony foundation of *L. apiculatum*. In this study, they studied the life cycle of this species under different conditions of humidity, temperature, and substrate. Ant queens were placed either in glass tubes with moist cotton or in jars with soil, and were held at varying temperatures and relative humidity. Observations of the time until different life cycle events occurred are summarized in Table 1. Observations of the longevity of the various reproductive castes of *L. apiculatum* are as follows: males lived 15 to 37 days, virgin queens lived 19 to 268 days and fertilized queens lived 17 to 316 days. However, the last estimate is incredibly short for a queen, so either these ants are highly polygynous or they live much longer in the wild. This study is a good start to give us an idea of the duration of different life cycle events and the life spans of each caste, however, further work is needed to understand the variability in time of these events under various conditions.

No such studies have been conducted with *L. occidentale* or *L. luctuosum*.

Table 1. Colony foundation of *L. apiculatum* modified from Conconi et al. (1983a).

Glass Tubes		Jar with Soil	
32°C/ 70-80% RH		26°C/ 40-50% RH	
Event	Time (days)	Event	Time (days)
First eggs	11.00 ± 2.3	First eggs	27.80 ± 6.9
First pupa	9.61 ± 2.1	First pupa	24.20 ± 6.2
First larva	9.84 ± 2.4	First larva	25.16 ± 7.8
First adults	28.23 ± 4.0	First adults	70.83 ± 11.3
Total	28.23 ± 5.0	Total	70.83 ± 11.4

Associations and Mutualisms

Beetles belonging to the Family Staphylinidae including *Sceptobius schmitti* Wasmann, *Dinardilla liometopi* Wasmann, *Dinardilla mexicana* Mann, and *Sceptobius dispar* Sharp have been found within the nests of *L. apiculatum* (Gregg, 1963a; Danoff Burg, 1994). "*Dinardilla mexicana* and *S. dispar* currently co-occupy *L. apiculutiim* nests on the eastern part of the Mexican plateau, while *S. schmitti* and *D. liometopi* are found together in nests on the western part of the Mexican plateau and then north to Colorado. More collecting should be done in the central part of the Mexican plateau to determine whether there is a zone of overlap between these two geographical species groups" (Danoff Burg, 1994). The staphylinid *Liometoxenus* was first described from specimens found foraging next to colonies of *Liometopum luctuosum* and *L. occidentale* (Kistner et al., 2002; Del Toro et al., 2009). A weevil *Liometophilus manni* Fall has also been discovered in the galleries of *Liometopum apiculatum* in southern Arizona and Mexico (Mann, 1914). The impact or role of these beetles on the ants is unknown.

Figure 1. Insulation removed by *L. luctusosum* in a mountain home in the San Bernardino Mountains, CA.

Dinardilla and *Sceptobius* beetles are also often observed alongside foragers or in nests of *L. occidentale*. *Sceptobius lativentris* (Fenyes) is only found with *L. occidentale*, this is unique among the Sceptobiini (Danoff Burg, 1994). More collecting needs to be done in nests of *L. occidentale* to determine the current geographic distribution of *S. lativentris* (Danoff Burg, 1994).

All members of the genus *Sceptobius* are quick moving, long-legged beetles that interact with their ant hosts by running up to groups of ants, briefly grooming a number of them, and then running away to the periphery of the ant nest (Danoff Burg, 1994). *Dinardilla mexicana* and *D. liometopi* interact actively and, in some cases, aggressively with some host ants. Typically, one of these beetles approaches a stationary host ant from the side and begins grooming the ant's legs with its mouthparts, after which the beetle mounts the ant and grooms its dorsum. This interaction can last from 3 minutes to 20 minutes and is likely used to spread the cuticular hydrocarbons that specify the colony odor from the ant to the beetle (Danoff Burg, 1994).

The staphylinid *Liometoxenus* was first described from specimens found foraging next to colonies of *Liometopum luctuosum* and *L. occidentale* (Kistner et al., 2002; Del Toro et al., 2009).

Liometopum also have mutualistic relationships with both plants and other insects. One example is the mutualistic relationship of *L. apiculatum* with the cholla cactus *Opuntia imbricate* (Haw.). This species has been seen protecting the cacti from herbivores and seed predators as well as foraging on extrafloral nectars (Miller, 2007). *L. apiculatum* tends the aphid *Cinara* sp. 1 found on *Pinus rudis* Endl. and the aphid *Cinara* sp.2 found on *Juniperus deppeana* Steud. (Velasco et al., 2007).

Structural Pests and Their Control

When *Liometopum* ants nest inside structures they can produce considerable amounts of frass consisting of chewed wood and insulation (Fig. 1). The excavations of these ants, however, are of a finer texture than those of carpenter ants (Fig. 2) and the frass is also much finer (Fig. 3). Attempts to eradicate nests indoors are often unsuccessful because foragers may congregate in hollows within insulation and wood, forming temporary 'resting places,' which are mistaken as nests (Klotz et al., 2008).

Velvety tree ants are best managed by locating and treating all colonies around the structure (Hedges, 1998). Inspect for nests and foraging trails in or around wood such as stumps, trees, or landscape timbers (Hansen & Klotz, 1999). These ants are attracted to water-damaged wood, but nests can also be found in dry, sound wood and foam insulation. Night inspections might be helpful during summer months as these ants are more active at night (Klotz et al., 2008).

A combination of baits and sprays should be used in an IPM program to successfully manage these ants. Baits containing a sweet food attractant should be applied in or near foraging trails first, allowing time for the ants to carry the bait active ingredient into the nest. Then dusts and sprays may be applied. Dust formulations may be used by PMPs to treat "resting" areas or satellite nests within structures (Hedges, 1998; Klotz et al., 2008).

Re-entry by undetected colonies outside a structure can be prevented with a perimeter spray around the foundation of the structure (Hedges, 1998; Klotz et al., 2008).

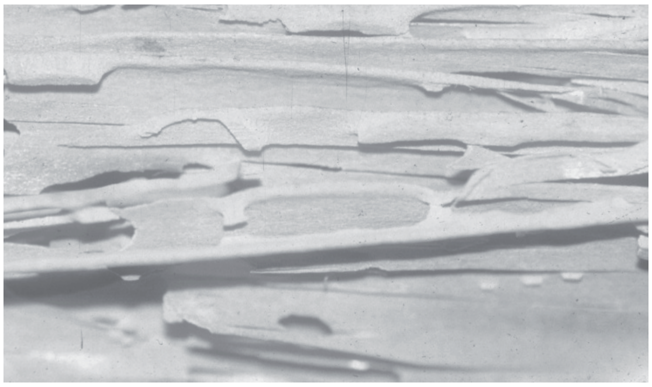
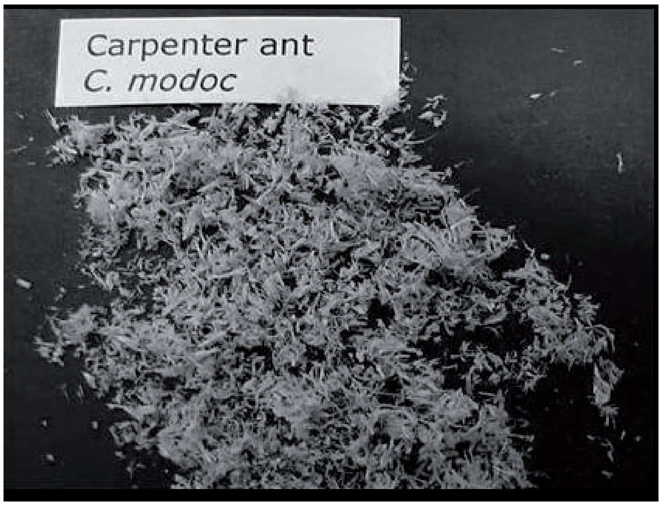
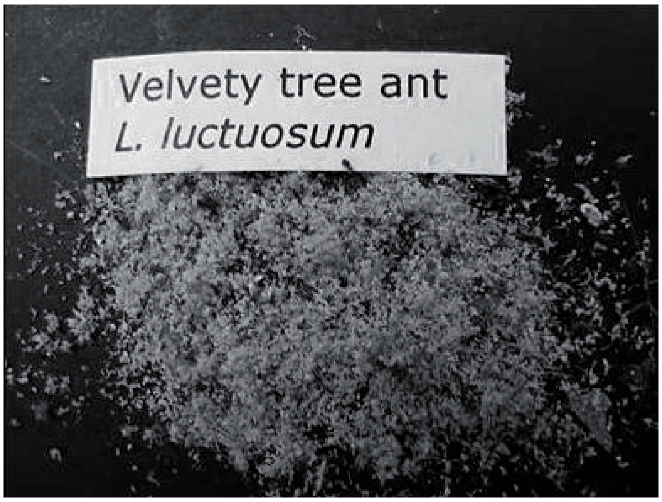


Figure 2. Damage to wood caused by workers of the *L. occidentale*.



A



B

Figure. 3. A – Frass produced by *Camponotus modoc*. B – frass produced by the carpenter ant *L. luctuosum*.

Foraging trails outside the structure in the surrounding landscape, on utility lines, or on the trunks of trees should also be sprayed. Trees in which the ants may be nesting are also target areas for treatment (Klotz et al., 2008).

Access into the structure should be eliminated by trimming trees and shrubs that are in contact with the structure or wires and cables leading into the structure (Klotz et al., 2008). Entry points around windows, doors and fixtures should be sealed.

Ants located in dead wood are best eliminated by removing infested wood; however, this is not always possible. Another treatment option is to drill and inject a small amount of insecticide dust labeled for this application into the galleries. Ants located in firewood can be eliminated by discarding or burning the infested wood. Never treat firewood with residual insecticide (Hedges, 1998)! Ants located in the soil under rocks and stones can be treated by thoroughly drenching the nest with residual insecticide (labeled for such use) using a compressed air sprayer (Hedges, 1998).

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