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A Supercolony of the Thatch Ant *Formica obscuripes* Forel (Hymenoptera: Formicidae) from the Blue Mountains of Oregon

Abstract

Foliage-foraging ants have often been demonstrated to be important predators of tree defoliating insects such as western spruce budworm. Because of the importance of ants as pest suppression agents, we were interested in describing a rare supercolony of western thatching ants (*Formica obscuripes* Forel) from the Blue Mountains of northeastern Oregon. The supercolony occupies a site within a second-growth mixed-conifer stand near Lehman Hot Springs, approximately 20 km east of Ukiah. Umatilla County, Oregon. In October 1993, the 4-hectare colony had 210 active nests, with the largest nest having an aboveground volume of 6 m³. Location of primary nests was not related to canopy cover, although nests tended to be associated with stumps and down woody debris. Nest excavations in May and June 1995 allowed estimation of the total nestbound population for the supercolony at 56 million individuals; addition of the foraging population would increase this estimate substantially. We estimate that to maintain the current worker population the supercolony would require at least 470 kg dry weight of food from its foraging territory annually, or about 11 times the total dry weight of western spruce budworm that might typically occupy the site at any given time during an outbreak. Thatching ants may have had a significant effect on populations of defoliating insects at Lehman Hot Springs during the last western spruce budworm outbreak (1980-1992), since the forest stand occupied by the supercolony was visibly less defoliated than the surrounding mixed-conifer stands.

Introduction

Species of the Formica rufa-group (thatching ants of North America and red wood ants of northern Europe and Asia) have received considerable attention as predators of forest pests. Thatching ants are ecologically dominant ants that tend Homoptera for honeydew, as well as scavenge and prey on a wide variety of terrestrial arthropods (Weber 1935, Cherix and Bourne 1980, Skinner 1980, MacKay and MacKay 1984). In mixed conifer forests of Europe, rufa-group species have historically been encouraged for their beneficial effects in controlling populations of forest insect pests (Otto 1962, McNeil et al. 1978). Their beneficial influence is documented in North America as well, as predators of western spruce budworm (Choristoneura occidentalis Freeman)(Youngs and Campbell 1984, Torgersen et al. 1990), and gypsy moth (Lymantria dispar (L.))(Smith and Lautenschlager 1981).

In North America, Europe, and northern Asia, colonies of at least 13 *Formica rufa*-group species have been reported to exhibit "polydomy," in which the colony is composed of more than one primary nest (Marikovsky 1962, Talbot 1971, Imamura 1975, Higashi and Yamauchi 1979, Mabelis 1979, Rosengren 1979, Cherix and Bourne 1980, Kloft et al. 1973, MacKay and MacKay

18 Northwest Science, Vol. 71, No. 1, 1997 © 1997 by the Northwest Scientific Association. All rights reserved. 1983, Wheeler and Wheeler 1986, Rosengren et al. 1985, O'Neill 1988). In general, small colonies composed of fewer than about 100 nests are termed "supranests," while larger colonies occupying hundreds of nests are termed "supercolonies" (Rosengren et al. 1985).

This paper describes a supercolony of 210 nests of the western thatching ant *Formica obscuripes* Forel in the Blue Mountains of northeastern Oregon. We addressed four objectives intended to identify the function of thatching ants in the forest ecosystem and the potential factors affecting their local distribution and abundance: 1) confirm colonial status, 2) describe the abundance and distribution of nests, 3) estimate total population size during the study period, and 4) determine the relation between forest structure and the distribution and abundance of nests. We also sought to determine whether other such populations of nests might exist in similar mixed-conifer stands elsewhere in the local geographical area.

Study Area and Species

The 4-ha study site is near Lehman Hot Springs (T5S, R33E, Sec. 12), about 20 km east of Ukiah, Umatilla County, Oregon. The mixed-conifer stand

within which the site lies was dominated by grand fir (Abies grandis (Dougl. ex D.Don) Lindl) with a heavy component of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco). The plant association at the site was grand fir/twinflower (CWF3 21 ABGR/LIBO-BLUE of Johnson and Clausnitzer 1992, pers. comm. F. C. Hall, USFS Plant Ecology Program). The site is on private land owned by the Lehman Hot Springs Development Corporation, which operates the hot springs as a recreational facility. The assemblage of nests was bounded on the north by a small abandoned sawmill in a clearing. Immediately to the east was the commercial recreation site associated with the hot springs. To the south and west were intensively managed stands of mixed conifers interrupted by a few logging roads. Many of the nearby stands were recently logged to harvest trees killed during an outbreak of western spruce budworm that ended in 1992.

Materials and Methods

Supercolony status was assessed in May 1995 by transferring workers among primary nests, and by observation of active trunk trails. For each transfer, a worker from the surface of the source nest was herded into a clean vial without direct handling and was held for at least 5 minutes before introduction to a different primary nest. We performed three sets of transfers of workers: 1) among nests within the 210-nest supercolony, 2) from an adjacent population of nests 300 m north to nests within the study population, and 3) from a Grande Ronde Valley colony of Formica obscuripes 50 km east of Lehman Hot Springs to nests within the study population. We assumed supercolony status if the following results were obtained: 1) transfers among nests within the Lehman supercolony did not result in worker rejection, 2) transfers from other populations resulted in rejection, and 3) primary nests within the supercolony were linked by a common trunk trail system.

To describe nest distribution, we laid out a 200-X 200-m (4 ha) study area, on 23 September and 7 October, 1993. Area boundaries were laid out to encompass the apparent extent of the supercolony. Study area boundaries were laid out with hand compass and marked with wire flags at 20-m intervals. We used compass and string lines to lay out intermediate grid-lines to form 100 20- X 20-m plots. Corners of plots were marked with wire flags. The location of nests within each plot was sketch-mapped. For each nest we recorded height, longest and shortest diameters, activity status (active-vigorous nest surface activity; declining-nest surface with few workers present; dead-no activity on nest surface), and classified the kind of wood, if any, with which the nest was associated (live tree, dead tree, stump, down wood). To examine the relation between forest structure and the distribution and abundance of nests, tree-crown closure was measured with a spherical densiometer at the center of each plot (Lemmon 1956). Four measurements of crown closure were made, each facing toward a side of the plot, and the mean of the four measurements was used to characterize crown closure within each plot. Regressions were calculated for crown closure means against both nest volume and number of nests per plot. The spatial pattern of ant nests was analyzed with nearest neighbor analysis, with the use of the refined nearest neighbor program (Moeur 1993, 1995).

To approximate nest shape for determining aboveground volume of nests, we measured height and long and short diameters. We assumed that nests were symmetric, with an elliptic base and parabolic profiles along the perpendicular planes running parallel to the major (x-y) and minor (yz) axes of the ellipse (Figure 1). Other shapes were considered, but the elliptic-paraboloid model yielded nest shapes that were most visually faithful to the general shape of the nest.

We derived the equation for volume (V) as a function of nest height (h), 1/2 long diameter (l), and 1/2 short diameter (s):

$$V(h,l,s) = \frac{4}{3}hs \int_{-l}^{l} \left[1 - \left(\frac{x}{l}\right)^2\right]^{\frac{3}{2}} dx$$

To calculate nest volumes, we integrated this equation to yield:

$$V(h,l,s) = \pi \times \frac{h \times l \times s}{2}$$

To correlate nest volume and worker population we excavated six primary nests in May and June 1995. Nest material occupied by ants was



Figure 1. The elliptical-paraboloid shape used to compute aboveground volumes of ant mounds. V, volume; h, height; l, 1/2 long diameter; s, 1/2 short diameter; x, y, z axes.

pitchforked and shoveled into large PVC-coated nylon "dry bags"^{1,2}, mixed thoroughly, and weighed. Aboveground and belowground nest material was placed in separate bags. Three approximately 1-liter sub-samples each from aboveground and belowground nest material were then removed and weighed. In the laboratory, eggs, larvae, pupae, workers, and reproductives were sorted from the subsamples and counted. Mean counts from subsamples were then multiplied by the quotient of total nest weight and total subsample weight to obtain nestbound population sizes. A regression was calculated for aboveground volumes versus nest populations, and the resulting equation was used to estimate the population of each of the 210 active nests, the summation of which provided an estimate of population for the entire supercolony.

Assuming that nestbound population size was correlated with forager activity, the relation between mound volume and nestbound population size could be used to create an approximate visual image of forager activity at the site. Population sizes of active mounds were used as a third (vertical) dimension along with the x-y coordinates of nest locations to create the visual display. Population sizes were graphed with SigmaPlot for Windows (Jandel Scientific, 1994)². The first step was to create a mesh-surface fit to the population at a high enough resolution to obtain a relatively smooth surface, with peaks and troughs reflecting areas of high and low forager activity. A contour graphing option was then selected on the mesh points of location versus forager activity. A log scale was used on the forager activity axis (reflecting the 3-dimensional nature of this quantity) and different line-densities were chosen for the major and minor contour intervals. The resulting image gives an approximation of nest distribution and forager activity at the site.

To determine whether supercolonies such as the Lehman colony might occur elsewhere in Blue Mountains mixed-conifer forests, we conducted a census on 161 km of transects. We selected varied locations for the transects within the Umatilla National Forest so that they would be representative of a range of habitats. Twelve transects (10 meters X 4 to 22 km) were examined between 7 and 21 October, 1993. Transects were laid out along the U.S. Forest Service road system within

¹76.2 X 152.4 cm; "guitar bag"; 18 oz. nylon. Available from Cascade Outfitters, Springfield, Oregon, 97477.

²Mention of product or source is given for information only. It does not constitute endorsement of either by the U.S. Government.

Townships 4-6 S., and Ranges 29 and 30 E., about 20 km west of Ukiah, and 30 km northwest of the study colony. The area traversed was associated with the roads from Happy Home Spring to Thompson Flat Well on the west side of the area, and from Gulliford Spring to Divide Well on the east. A single examiner then walked along the transect, which was simply a walking-course that maintained a minimum distance of 200 meters from any road, and the area within 5 meters on each side of the transect was scanned for thatching ant nests.

Results

The total of 12 transfers among nests within the Lehman population typically resulted in resident worker acceptance of the introduced workers. In general, introduced workers were either ignored for parts of the 5-minute observation period, experienced occasional antennation from resident workers, and/or entered a nest entrance hole and disappeared. Of the four introduced individuals observed for the full 5-minute period, two experienced mild "mobbing" behavior by resident workers, in which several resident workers showed considerable interest but no aggressive behavior toward the introduced worker. To compare withinnest to among-nest behavior, we removed a number of nest-surface workers, held them for 5 minutes, and reintroduced them into their own primary nests. We observed no difference in the response of resident nest surface workers to resident re-introduced workers, compared to the response of residents to workers from other nests within the Lehman population-within-nest introductions also resulted in mild "mobbing" behavior, as well as occasional antennation and trophyllaxis.

By contrast, nest surface workers of the same species introduced from the Grande Ronde Valley population 50 km away were immediately attacked by resident workers, with each introduced worker attracting a locus of several residents. Attack consisted of pinioning and biting of introduced workers by resident workers, with introduced workers responding by biting and spraying from the poison gland. An intermediate response by resident workers was observed when nest-surface workers were introduced from the adjacent population 300 m north of Lehman Hot Springs. Upon transfer, introduced workers were immediately pinioned by resident workers for each of the seven 5-minute observation periods. Pinioning was not however, accompanied by additional aggressive behavior either on the part of residents or introduced workers. In summary, transfer experiments supported the hypothesis that the Lehman population was a "supercolony," and not a population of independent nests. The graded responses of resident workers to introduced workers from colonies 300 m and 50 km distant suggests that the adjacent population may be closely related to the Lehman population, perhaps owing to past nest fission events.

We also observed a complex network of trunk trails among nests within the Lehman population, with foragers moving freely along trails among nests. Transport of larvae, pupae, and adults along trunk trails was also observed, usually in one direction at any given moment of time. Hence, both transfer experiments and trunk trail observations strongly support the hypothesis that the Lehman population is a supercolony.

A total of 293 nests were recorded during the nest census, of which 210 were occupied by workers (Figure 2). Of the 210 occupied nests, 8 had aboveground volumes greater than 1000 liters, 92 ranged between 100 and 999 liters, 96 between 10 and 99 liters, and 14 were less than 9 liters in aboveground volume. The largest nests occurred in an arc from the southwest corner northward and then east toward the northeast corner. Fiftyone of the 100 20-meter plots contained fewer than two nests, while only eight contained more than six nests, giving the nests a left-skewed distribution at the 20 x 20 meter plot scale. Nearest neighbor analysis revealed clumping of nests at the scale of 3 to 12 meters (Figure 3). Observed nest distribution merged with the theoretical random distribution at scales of less than 3 meters and greater than 12 meters. Among active nests there was no relation between canopy cover and nest volume. Of the 210 active nests, 99 (47%) were associated with large down logs or slash (logs< 3 cm in diameter); these nests were also the largest in volume (312.0 liters \pm 79.5 S.E.). There were 49 active nests (23%) located on stumps or against the bases of living trees, having only about half the volume (158.0 liters \pm 34.0 S.E.) of the largest nests. The third group of 62 nests (29%) were not associated with any woody structure and were intermediate in aboveground volume (187.0 liters ± 26.0 S.E.).



Figure 2. Distribution, aboveground nest volume size classes (in liters) and health status of ant nests at Lehman Hot Springs, Oregon, 1993. Symbols denote ranges of aboveground volume (liters) of nests calculated by Equation 2. Inset indicates area of supercolony shown in Figure 5.

A total of six primary nests were excavated in May and June 1995. We counted between 0.9% and 3.5% of the total individuals within each nest. The aboveground volumes ranged from 13.8 to

239.9 liters (Table 1). Proportions of the four developmental stages of ants varied considerably among excavated nests, with only two nests having an abundance of all stages. In general, we

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Figure 3. Cumulative nearest neighbor distribution for the 210 active thatching ant nests at Lehman Hot Springs, with $F_{(d)}$ = the proportion of nests having a nearest neighbor within distance d. Theoretical random distribution is given with a 95% confidence envelope, and a uniform distribution is provided for comparative purposes.

found more brood in the latter three excavations. Reproductives were found in four of the six nests; many of the queens had evident wing stumps, indicating that these had recently mated and been accepted into the nests. There was a significant correlation (y = 0.944x + 42.93; $r^2 = 0.56$) between aboveground nest volume and the estimate of total nestbound population (Figure 4). The nest excavated first had a significantly greater nestbound population than the nest of equivalent size excavated three weeks later. Without this early outlier, the r^2 for the latter set of five excavated nests was 0.93, rather than 0.56. The most conspicu-

ous difference between the first excavation and the latter five was the weather—through most of April and early May conditions were cool and wet, but they changed to warm and dry by mid-May. During the latter half of May, the amount of worker activity on the surface of most nests declined substantially, probably because many workers were moving out into their foraging territories. Hence the early May excavation may have contained a large number of nestbound workers that had not yet left the nest for foraging duties.

When the correlation equation is applied to all 210 active nests, the estimate for the total nestbound population of the supercolony is 56,400,000 individuals, including sexuals and all developmental stages. Because foraging populations were not estimated, this figure can be considered a conservative estimate of supercolony population. Of the 210 active nests, 76 had estimated populations of between 10,000 and 99,000 individuals, 127 had between 100,000 and 999,000, and 7 nests were estimated to contain more than one million thatching ants. The largest nest had a volume of more than 6 m³ and an estimated population of 6.1 million individuals.

After nest volumes were converted to nestbound ant numbers, a contour map was generated that depicts ant density within the supercolony (Figure 5). Assuming that the number of nestbound individuals reflects potential foraging activity, the contour map depicts the predicted spatial ecological effect of the supercolony.

The 161 km of nest-detection transects traversed diverse stand types and habitats: mixed-conifers, ponderosa pine, lodgepole pine, variants of these stands, riparian corridors and uplands, grassy scabflats, and edges. No thatching ant nests were found in the census,

TABLE 1. Aboveground nest size (liters), percent of total nest population counted (%Count), and estimates of eggs, larvae, pupae, workers, and queens for six nests excavated at Lehman Hot Springs study site, 9 May through 9 June 1995.

Nest	Date	Size (liters)	%Count	Eggs	Larv	Pup	Wrkrs	Queens	Total
1	9 May 95	66.5	1.75	0	0	0	236,000	500	236,500
2	22 May 95	65.4	2.09	0	190	0	36,900	0	37,090
3	22 May 95	13.8	3.50	0	0	0	17,400	100	17,500
4	31 May 95	239.9	0.90	7,980	10,800	3,430	223,000	1,020	246,230
5	9 June 95	148.2	1.94	1,040	17,800	10,200	169,000	180	198,220
6	9 June 95	38.5	3.33	1,790	340	0	59,200	0	61,300

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ADUVE-GROUND NEST VOLUME (IITers)

Figure 4. Correlation between aboveground nest volume and the number of nestbound individuals (data from nest excavations).

Discussion

Supercoloniality appears to be a plastic feature of most Formica rufa-group species. Both single nest colonies and supercolonies have been observed in at least 13 F. rufa-group species worldwide, including all of the species most intensively studied. Supercolonies range in size from a few nests (MacKay and MacKay 1983), to dozens of nests (Rosengren et al. 1985), to colonies composed of hundreds or even thousands of nests (Higashi and Yamauchi 1979). Supercolonies can occupy relatively small areas with a few large nests. For example, in Russia, Marikovsky (1962) found 111 nests with 140 million F. rufa individuals on 0.61 ha. In contrast, supercolonies can occupy more sparsely very large areas as described by Higashi and Yamauchi (1979), who tallied 45,000 nests with 306 million F. yessensis individuals on 2.7 km² in Japan. Presumably, differences in worker density are related to habitat type; the F. rufa supercolony described above was found in a forested habitat, while the *F. yessensis* supercolony occurred in a grassland. In support of this observation, the forest-dwelling supercolony described herein is much more similar in worker numbers, nest numbers, and area occupied to the forest-dwelling *F. rufa* colony described by Marikovsky.

Because supercolonies are composed of nests among which workers cooperate, the spatial arrangement of nests will be expected to differ from the situation in which individual nests compete. Indeed, the aggregated nest distribution within the Lehman supercolony may represent a history of reproduction by nest fission, and subsequent cooperation among nests, with the scale of aggregation (3-12 meters) reflecting the distance daughter colonies migrate from their parents. This among-nest aggregation contrasts sharply with the "over-dispersed" distributions observed in nearly all studies of ant populations composed of competing nests (Levings and Traniello 1981). Hence, overdispersion is the rule when among-nest



Figure 5. Contour map illustrating worker activity derived from correlation of nest volume and nest population size for the 100-X 100-meter area dilineated in Figure 2. Contours equal ants X 1,000.

territoriality occurs, while among-nest aggregation may be a general feature of supercoloniality.

Supercoloniality may increase colony fitness under certain conditions. Because supercoloniality results in decentralized foraging, energetic and microclimatic constraints imposed by a fixed central place are relaxed, allowing foraging range expansion (Rosengren and Pamilo 1983, Puntilla et al. 1994), increased domination of resources (Higashi and Yamauchi 1979, Cherix and Bourne 1980), and more economic defense of territory (Hölldobler and Lumsden 1980). Links among widely dispersed nests may also facilitate communication about food, disturbance, and potential new nest sites (Scherba 1964).

Several authors have observed differences in seasonal use of nests within supercolonies of *F. rufa*-group species, with larger nests occupied yearround and smaller nests occupied during the foraging months (Marikovsky 1963, Talbot 1971, Ito 1973, MacKay and MacKay 1983, Rosengren et al. 1985). Excavations at our study site support this observation, with some nests containing neither brood nor queens in late spring (see Scherba 1961, Rosengren et al. 1985). This "division of labor" at the scale of the nest may provide the supercolony with temporal flexibility, allowing it to expand when food resources are available in the summer and contract to more insulated nests for protection during the winter months (Rosengren et al. 1985). A long-term advantage of supercoloniality is that multiple nest sites may buffer the colony from catastrophic environmental change, which would decrease the probability of colony extinction (Pamilo and Rosengren 1983).

The plastic nature of F. rufa-group species with respect to supercoloniality is a direct consequence of the tendency for workers to accept newly mated queens, and the subsequent use of fission as a primary mode of colony reproduction (Kloft et al. 1973, Ito and Imamura 1974, MacKay and MacKay 1983, Hölldobler and Wilson 1990). Evidence of worker acceptance of queens was clear from the present study as well, with two excavated nests containing numerous de-alated queens deep within nest interiors. Hence supercoloniality in F. rufa-group species, with its reliance on asexual reproduction, is analogous to facultative apomixis in plants, in which the colony can suspend outbreeding and independent nest founding whenever environmental circumstances are appropriate: i.e. when sufficient local resources are available and/or dispersal to more distant alternate sites is less profitable (Hölldobler and Wilson 1990). From this argument, we suggest that the mixed-conifer stand at the Lehman site offers relatively stable and abundant food and an abundance of nesting sites for thatching ants in comparison to adjacent forests.

Because of their large population and biomass, F. rufa-group colonies can have profound effects on ecosystems in which they live. Potential effects include serving as prey for and competitors of vertebrate species (Gosswald 1990, Haemig 1992), influencing the growth of trees (Rosengren and Sundstrom 1991), and modification of forest soils (Oinonen 1956, Beattie and Culver 1977, Petal 1978). Possibly the greatest documented effect of F. rufa-group species is on the abundance and distribution of other invertebrate species, including nest inquilines (Gosswald 1989; William Clark pers. comm.), predators (Cherix and Bourne 1980), and other ant species (Higashi and Yamauchi 1979, Cherix and Bourne 1980, MacKay and MacKay 1982, Savolainen 1989, Puntilla et al. 1994). In addition, the function of *F. rufa*-group species for suppression of insect pest populations has received considerable attention in Asia (Ito and Higashi 1991), in Russia (Grimalski 1959), in Europe (Wellenstein 1952, Laine and Niemela 1980), and in North America (Torgersen et al. 1990). With few exceptions (e.g. *Ips typographus*, Diachenko 1991), *F. rufa*-group species have typically been implicated in population regulation or suppression of lepidopteran (McNeil et al. 1978, Ito and Higashi 1991, Laine and Niemela 1980, Skinner and Whitaker 1981) and sawfly (Baranov 1971) populations.

While other insectivores such as spiders and birds may be capable of reducing forest defoliator populations during their endemic stage and of delaying the onset of defoliator epidemics (Mason 1987), thatching ants may be unique in their power to reduce populations of defoliators in localized areas during the outbreak phase. This power is due not only to their great relative abundance, but also to their propensity to switch to common food as it becomes abundant (Horstmann 1972). Suppression power can be illustrated by estimating the food requirements of the Lehman supercolony and comparing this to an estimate of the food represented by western spruce budworm during outbreak conditions. Although the annual metabolic energy requirement for a supercolony of 56 million individuals is enormous, probably most of this energy is obtained by workers tending aphids and scales for honeydew (Skinner 1980). Thatching ants, however, require insect protein to rear new workers (Skinner 1980). If we assume mean worker dry weight of 2.5mg, a gross production efficiency of 10%, and a mean worker longevity of 3 years (Elton 1977), then the colony of 56 million workers would require about 470 kg dry weight of food annually to replace itself. When this annual food requirement is compared to the potential biomass available during a western spruce budworm outbreak, the power of the supercolony for pest suppression is evident. A stand inventory at the Lehman site conducted in July 1995 indicated 204 stems/ha > 15 cm in diameter, and 598 stems/ ha < 15 cm diameter. This gives an estimate of 85,390 m² of foliage for the study site (Wykoff et al. 1982; Crookston et al. 1990; Crookston 1991). If budworms were to occupy the Lehman site at their maximum observed densities in the Blue Mountains (e.g., 105.6 larvae/m² of foliage; Torgersen et al. 1993), a total of 9.02 million budworm larvae would be present at any given time within the study area, for a total dry weight of 43 kg (4.75 mg average dry weight for 4th instar). This is just 30.4% of the total thatching ant biomass at the site, and just 9.0% (43/470kg) of the total estimated food requirement of the thatching ant supercolony for a single year.

While these figures illustrate the potential for thatching ants to control outbreak budworm populations, no one has experimentally demonstrated pest suppression of this kind. Observations do suggest however, that trees or stands with large populations of thatching ants or red wood ants experience less defoliation than trees or stands lacking them (R. Mason, pers. comm., Laine and Niemela 1980). At Lehman Hot Springs for example, most of the mixed conifer stands adjacent to the study site had suffered heavy defoliation and tree mortality during the recent 10-year outbreak, while most of the trees at the supercolony site itself remained green and relatively healthy.

These observations suggest that where they are common, thatching ants can play an important role in suppression of insect pest populations. Yet

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for no known reason, species of the *F. rufa*-group are not now common in the mixed-conifer forests of the Blue Mountains. Our 161-km transect across a variety of stand types, conditions, and terrains yielded not one thatching ant colony. Because *F. rufa*-group ants are a potentially important feature of healthy mixed-conifer forests in the Blue Mountains, future research should focus on the factors that explain their low overall numbers and their patchy distribution.

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