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A FIELD STUDY OF THE NESTING ECOLOGY OF THE THATCHING ANT, FORMICA OBSCURIPES FOREL, AT HIGH ALTITUDE IN COLORADO

John R. Conway¹

ABSTRACT.—A field study of the thatching ant, Formica obscuripes Forel, at 2560 m elevation in Colorado provided information on mound density, composition, dimensions, and temperatures; worker longevity; and mite parasitization. Density was 115 mounds/ha. Mounds had 1–52 entrances and *Peromyscus* fecal pellets in the thatch. Mounds conserved heat and exhibited thermal stratification. Excavations of 4 nests revealed depths of 0.3 m to almost 1 m, novel myrme-cophiles, and 0–198 wingless queens per nest. Marking experiments demonstrated that some workers overwinter and live more than a year.

Key words: Formica obscuripes, thatching ant, Colorado, ant mounds, myrmecophiles.

Formica obscuripes Forel is in the Formica rufa-group (Weber 1935) and ranges from Indiana and Michigan westward across the United States and southern Canada. It is one of the most abundant ants in western North America, especially in semiarid sagebrush areas (Gregg 1963), and has been found at altitudes up to 3194 m (Wheeler and Wheeler 1986). The objective of this field study was to compare mound density, formation, composition, dimensions, and temperatures, worker longevity and parasitization, nest depths, myrmecophiles, and the number of wingless queens per colony of this species at high altitude in Colorado with findings from lower altitude studies in Colorado (Jones 1929, Gregg 1963, Windsor 1964), Idaho (Cole 1932), Iowa (King and Sallee 1953, 1956), Michigan (Talbot 1972), Nevada (Clark and Comanor 1972, Wheeler and Wheeler 1986), North Dakota (McCook 1884, Weber 1935), Oregon (McIver and Loomis 1993, McIver and Steen 1994), Washington (Henderson and Akre 1986), and Canada (Bradley 1972, 1973a, 1973b). Although this species seems to be most common at altitudes of 1524-2743 m in the mountainous states (Gregg 1963, Wheeler and Wheeler 1986), the highest previous study site was at an elevation of 1550 m (Clark and Comanor 1972). It is hypothesized that climatic and vegetational changes associated with higher altitude may alter the nest ecology of this species.

MATERIALS AND METHODS

The study site is in Gunnison County north of Blue Mesa Reservoir and west of Soap Creek Co. Rd. in western Colorado at an altitude of 2560 m. Field observations were con-

ducted 5–6 August 1990, 20 June –11 October 1992, 28 June–16 August 1993, 29 June–31 July and 14–16 August 1994, and 3, 29–31 July and 15–16 August 1995. The area, dominated by big sagebrush (*Artemesia tridentata* Nuttall) and to a lesser extent by rubber rabbitbrush (*Chrysothamnus nauseosus* [Pallas] Britton), is adjacent to a grove of quaking aspens (*Populus tremuloides* Michaux).

The locations of 85 mounds were mapped in a study area (64.6 m \times 114 m) using a surveyor's transect and compass in July 1993 to determine density.

The diameters and heights of 97 mounds in the study area and surrounding area were measured. The number of entrances per mound was determined by inserting sprinkler flags into the active openings on each mound.

Mound temperatures were measured with a Model 100-A VWR digital thermometer probe. Sixty-seven temperature measurements were made on 34 mounds in the evenings (1915–2045 h) 2–14 July 1993 by inserting the probe approximately 15 cm into the top of each mound. The temperatures of 4 of these mounds were also recorded in the afternoon (1538–1600 h)

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on 2 July 1993. In addition, hourly temperatures were recorded at 4 locations (air, ground, mound top, and mound base) for 3 differentsized mounds in July 1994 between 0700 and 2000 h to determine how mound size affects thermal dynamics. Temperatures were taken at a mid-sized mound (height = 25.4 cm, average diameter = 1 m) on 16–18 July, at a large mound (height = 49.5 cm, average diameter = 1.21 m) on 18 July, and at a small mound (height =27.9 cm, average diameter = 0.51 m) on 17 July. The small and mid-sized mounds were about 4.6 m apart and about 34-37 m from the large mound. The probe was inserted approximately 15 cm into the top, base, and ground adjacent to each mound. Temperatures were also recorded in the shade about 15 cm above the ground near each mound.

Hundreds of workers were marked on 8 mounds and 5 plants in 1992–93 by applying model airplane paint with a fine-tipped brush and by spraying 5 mounds in 1994 with colored acrylic enamel. Although many workers were incapacitated or killed, especially by spraying, most survived. Spraying was the most efficient technique for marking large numbers of ants. Four nests were excavated, 1 each on 6 August 1990, 27–28 June 1992, 12 July 1993, and 11–25 July 1994. The 1993 nest was poisoned with 1¹/₂ cups Hi-Yield ant killer granules (Diazinon) wetted down with about 7.6 L of water prior to excavation to investigate another technique for collecting queens and myrmecophiles. deer mouse (*Peromyscus maniculatus* [Wagner]) or vole (*Microtus* sp.). Thatch (n = 58) from 1 mound consisted mainly of small twigs 4–89 mm (mean = 24.19 mm) long and 1–5 mm (mean = 2.19 mm) in diameter. Workers were observed carrying fecal pellets into or out of mound entrances, but not on trails.

DIMENSIONS AND ENTRANCES.—The diameters of 97 mounds ranged from 19 cm to 142 cm (mean = 65 cm). Mound heights ranged from 6 cm to 58 cm (mean = 26 cm).

The number of entrances to 97 mounds ranged from 1 to 52 per mound (mean = 12), but their number, size, position, and activity changed over time. For example, 1 mound had 10 or more entrances in August but only 2 in October. Some entrances were larger than others, and some surrounded plant stalks growing out of mounds.

TEMPERATURES.—Measurements of moundtop and air temperatures in July 1993 demonstrated that mounds are warmer than air temperatures and that the differential is greater in the evening than in the afternoon. Evening temperatures (n = 67) for 34 mounds were $1.0^{\circ}-15.5^{\circ}$ C (mean = 8.6° C) warmer than corresponding air temperatures. Afternoon temperatures for 4 of these mounds were slightly warmer ($0.5^{\circ}-0.9^{\circ}$ C; mean = 0.7° C) than corresponding air temperatures.

RESULTS

Nest Density

The extrapolated density for the 85 mounds mapped in the 7364-m² area was 115 mounds/ ha. The closest mounds were 2.36 m apart.

Mounds

FORMATION AND COMPOSITION.—Mounds are composed of thatch and are usually dome shaped. Some mounds are exposed while others are overgrown or shaded by low vegetation. Dead sagebrush protruded from or was found on 63 of 98 mounds (64%). The largest mound was built around the base of a fence post. No mounds were found inside the aspen grove, but 2 were built around small aspen troos on the forest edge Hourly mound-top and mound-base temperatures recorded in July 1994 were almost always higher than ground temperatures, and top temperatures were warmer than air temperatures (Figs. 1–3). Differences in top and air temperatures were greater in the evening (1900–2000 h) for a large nest ($8.9^{\circ}-11^{\circ}$ C) and mid-sized nest ($6.8^{\circ}-14.4^{\circ}$ C) than their afternoon (1500–1600 h) differences, $2.6^{\circ}-6.3^{\circ}$ C and $0.6^{\circ}-8^{\circ}$ C, respectively. On the other hand, hourly top and air temperatures did not differ much for the small nest in the evening ($1.1^{\circ}-3.3^{\circ}$ C) and in the afternoon ($1.6^{\circ}-2.2^{\circ}$ C).

Average hourly top and base temperatures were higher than average air temperatures for the mid-sized and large mounds (Figs. 1–3). For example, average top and base temperatures were 6.2°C and 3.1°C higher than average air temperatures for the large mound and 4.6°C and 0.5°C higher for the mid-sized mound. However, for the small mound the average top temperature was actually 0.8°C lower, whereas the average base temperature was 2.7°C higher than the average air temperature.

trees on the forest edge. Mound thatch consisted mainly of twigs but also contained fecal pellets, probably from the

MOUND #3 JULY 16-18, 1994

MOUND #14 JULY 18, 1994



Fig. 1. Average mound-top, mound-base, ground, and air temperatures around a mid-sized *Formica obscuripes* mound from 0700 to 2000 h on 16–18 July 1994 at 2560 m in Colorado.

Hourly top and base temperatures showed thermal stratification. Average top temperatures were 3.2°C and 4.1°C higher than average base temperatures for the large and mid-sized mounds, respectively. However, for the small mound the stratification was reversed: average top temperature was 3.5°C lower than the average base temperature.

The poor thermal regulation of smaller mounds was also reflected by a greater fluctuation of hourly top and base temperatures. Daily ranges of top/base temperatures were 7.6/8.7°C, 13.3/15.9°C, and 13.8/26.3°C for the large, midsized, and small nests, respectively. Thus, larger mounds exhibited less daily temperature fluctuation than smaller mounds.

Worker Longevity

Fig. 2. Mound-top, mound-base, ground, and air temperatures around a large *Formica obscuripes* mound from 0800 to 2000 h on 18 July 1994 at 2560 m in Colorado.

d). However, 2 workers marked on a mound between 7–9 July and 15–27 July 1994, respectively, were observed on 30 July 1995 on another mound and on the original mound. Thus, some workers overwinter and live more than 1 yr.

Mites

Mite infestation was not common. Orange, spherical mites were noted on only 1 worker at 3 of the many mounds observed. The largest number of mites observed was 4–5 on the thorax and gaster of 1 worker.

Excavated Nests

Each of the 4 nests excavated contained numerous workers, larvae, and pupae, but the number of wingless queens per nest varied

Most marking experiments (n = 14) indicated greatly: 0, 1, 32, and 198. No winged reproduct that some workers live 19 to 44 d (mean = 31.6 tives were found except a male in 1 nest. The

MOUND #98 JULY 17, 1994



ers); and Lepidoptera (F. Noctuidae—larvae; Table 1).

DISCUSSION AND CONCLUSIONS

The extrapolated density of 115 mounds/ha is about 1.8 times greater than the highest density reported: 64/ha of Jack pine in Manitoba (Bradley 1973a).

Colonies are known to be polydomous and to reproduce by budding (Herbers 1979). Some primary mounds and small secondary moundlets along trails appeared and disappeared in our study area over the years as previously reported, and some may have moved. For example, a primary mound that was active in 1990 was largely deserted by 1994 and completely abandoned in 1995. Colonies have been reported to move at least 3 times during their life and to move 18 m from their original location, or 1.3–33 m after transplantation (Bradley 1972, 1973a). King and Sallee (1953, 1956) noted desertions of many old nests and the establishment of 1 or more new ones from each of them. All our mounds were in open sagebrush except for 2 built around aspens at the forest edge. Weber (1935) also noted that most mounds are in the open, but did find some mounds partially shaded and 1 enormous mound almost completely shaded in an aspen grove. In our study, 63 of 98 mounds (64%) showed evidence of being built around sagebrush as reported by Weber (1935), but a few were built around other structures such as trees and a fencepost. Weber noted that workers kill sagebrush by chewing bark at the base and spraying formic acid on the cambium. After 3 months, the stem is removed to form a longitudinal passage in the center of the mound leading to the main entrance. Weber (1935) reported that mounds are composed of slightly longer twigs (1-12 cm) than the ones we measured (0.4-8.9 cm), but these slight differences may simply reflect the availability of materials. A new discovery was the presence of fecal pellets of P. maniculatus or Microtus (Clark personal communication) on the surface and in the thatch of Colorado mounds. Since workers were never observed carrying pellets to mounds, their origin is unclear.

Fig. 3. Mound-top, mound-base, ground, and air temperatures around a small *Formica obscuripes* mound from 0800 to 2000 h on 17 July 1994 at 2560 m in Colorado.

depths of the nests were 0.3 m (estimated), 0.3 m, 0.64 m, and 0.97 m.

The nest excavated in 1993 contained the following arthropods: pseudoscorpions, collembolans, beetles and beetle larvae (1 *Ctenicera* sp. [F. Elateridae] and 4 *Eleodes* sp. [F. Tenebrionidae]; Table 1).

The following insects were identified in the 1994 nest: Collembola (F. Entomobryidae); Homoptera (F. Cicadellidae—1 immature, F. Aphididae—2 immatures); Hemiptera (F. Anthocoridae—1 specimen); Coleoptera (F. Curculionidae—5 adults, F. Scarabaeidae—1 adult and *Cremastocheilus* pupa and larval skin, probable F. Carabidae—1 adult, probable F. Anthribidae—2 larvae, F. Tenebrionidae—unidentified larvae, probable *Eleodes* sp. larvae, and *Eleodes* sp. pupae, F. Cerambycidae—Lepturinae, probable *Leptura* sp. larva); Diptera

(probable F. Asilidae—pupa); Hymenoptera (F. Formicidae—few *Tapinoma sessile* [Say] work-(1972), and Wheeler and Wheeler (1986)

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*Collembola (unident.) Weber (193	
*Homoptera	
*E Aphididae—-2 immatures	
*E Cicadellidae-1 immature	
*Hemiptera	
*F. Anthocoridae—1 specimen	
Diptera	
*F. Asilidae—pupa	
E Milichiidae	
Phyllomyza securicornis	Weber (1935)
E Leptidae—larvae	Weber (1935)
F. Anthomyiidae-larvae	Weber (1935)
F. Therevidac-larvae	Weber (1935)
F. Phoridac—larva	Windsor (1964)
Lepidoptera	Carl Carl (1997) - Carl (1992) Solar (199 2) - Carl (1997)
*F. Noctuidae—larvae	
Epizeuxis sp.—larvae	Weber (1935)
Hymenoptera	
F. Formicidae	
Lasius latipes Walsh	Weber (1935)
Leptothorax hirticornis Emery	Weber (1935)
*Tapinoma sessile Say	Weber (1935)
Thysanura—silverfish	Windsor (1964)
01	

TABLE 1. Arthropods in Formica obscu	ripes Forel nests	Coleoptera (continued)	
eported in the literature and identified	from 2 excavated	F. Scarabaeidae	
ests near Soap Creek, Colorado (*).		*Unident. adult	
	1711 (100x)	*Cremastocheilus sp.—pupa	
Collembola (unident.)	Weber (1935)	and larval skin	
*F Entomobryidae		Cremastocheilus wheeleri	
Homoptera		Le Conte—larvae	Windsor (1964)
*F. Aphididae—-2 immatures		Cremastocheilus wheeleri	
*F. Cicadellidac—1 immature		Le Conte—adults	Windsor (1964)
Hemiptera		Unident, pupae	Weber (1935)
*F. Anthocoridae—1 specimen		Euphoria inda L. in pupal cells	Weber (1935)
Diptera		Euphoria inda L. Jarvae	Windsor (1964)
*F Asilidae—pupa		Euphoriaspis hirtipes (Horn)—	(1000)
F. Milichiidae		larvae and adults	Windsor (1964)
Phyllomyza securicornis	Weber (1935)	Serica intermixta Bltch —adults	Weber (1935)
E Leptidae—larvae	Weber (1935)	Phullonhaga sm	Weber (1935)
F. Anthomyiidaelarvae	Weber (1935)	F Stanbylinidae	Weber (1000)
F. Therevidac-larvae	Weber (1935)	Tuchunorus californious	Monn (1011)
F. Phoridac—larva	Windsor (1964)	Philopthus callin Crow D dabilio	Mann (1911)
Lepidoptera		Cross P theorem to Horn	Walson (1025)
*F. Noctuidae-larvae		Caninga almosti Vista an	Weber (1955)
Epizeuxis sp.—larvae	Weber (1935)	Gonnisa alperti Kismer	Mackay &
Hymenoptera	(1000)		Mackay (1984)
E Formicidae		Goniusa obtusa Lec.	Weber (1935)
Lasius latines Walsh	Weher (1935)	Aderocharis corticinus Grav.	Weber (1935)
Leptothorar hirticornis Emery	Weber (1935)	Pacderinae (Gastrolobium or	TT 1 (100M)
*Taninana sessile Say	Weber (1935)	related genus)	Weber (1935)
Thysonuro_silverfich	Windsor (1964)	Platymedon laticollis Csy.	Weber (1935)
Coleoptera	(1004)	Small unident. adults	Windsor (1964)
Unident beetle nunu	Windson (1964)	F. Chrysomelidae	
E Elatoridao	Windson (1904)	Cryptocephalus sp.—larvae	Weber (1935)
*Cranicara un luma		E Hydrophilidae	
Malamotus an Jummu	Wahar (1025)	Berosus sp.	Weber (1935)
E Tanahai dan	weber (1955)	F. Cryptophagidae	
r. ienebrionidae	137 1 (1004)	Atomaria sp.	Weber (1935)
Unident. Jarvae and adults	windsor (1964)	F. Histeridae	
*Eleodes sp.—larvae and pupae		Hetaerius adult	Weber (1935)
*Unident. larvae		F. Anthicidae	
F. Carabidae	XX21 (100F)	Anthicus spadult	Windsor (1964)
Amara sp.—adult temale	Weber (1935)	Orthoptera	63 52
*Prob. adult	xxx 1 (1000)	F. Gryllidae	
Unident. adults	Windsor (1964)	Myrmecophila manni Schimmer	Henderson
*F. Anthribidae			and Akre (1986)
*2 prob. larvae		Arachnida	1940 COLUMN CONTRA 1962 EN 1960 (C
*E Cerambycidae		Small gray spiders	Windsor (1964)
*Prob. Leptura sp.—larva			and the second
*F. Curculionidae		*Pseudoscorpionida	
*5 unident. adults			

reported mound diameters within the range we observed (9-142 cm), Weber (1935) noted a much greater range (13–335 cm), but a smaller mean diameter (43 cm) than we found (65 cm).

Talbot (1972), Clark and Comanor (1972), and Wheeler and Wheeler (1986) noted mound heights in the range we measured (6-58 cm), but Weber (1935) reported lower heights (2.5-46 cm) and Henderson and Akre (1986) reported mounds up to 1.22 m high. Somewhat lower (20 cm) and higher (30 cm) mean heights were recorded by Weber (1935) and Wheeler and Wheeler (1986), respectively, than we found (26 cm).

The number, size, position, and activity of mound entrances changed over time as reported by Weber (1935). The number of entrances per mound in our study, 1–52, is close to the range of 3–50 per mound reported (Cole 1932, Wheeler and Wheeler 1986). In the early morning ants use openings in the sunlight; later as the temperature rises they use only shaded entrances as reported by Weber (1935). Henderson and Akre (1986) speculate entrances are opened during the day and closed with thatch at night to help control nest temperatures.

Our mounds, especially mid-sized and large ones, were generally warmer than ground and

air temperatures and exhibited thermal stratification from top to base. Weber (1935) and Andrews (1927) also noted that mounds are warmer than the ground, and Andrews reported that the upper parts are warmer than the lower parts of mounds. The differential between our mound-top and air temperatures was greater in the evening than in the afternoon. Small mounds showed a reversal of thermal stratification and greater hourly fluctuation of top and base temperatures, which is indicative of poorer thermal regulation.

Marking experiments suggest that worker longevity is often short but that some workers overwinter and live more than a year. Little information is available on the longevity of worker ants and none was found for this species. Although maximum longevity is known to be 3 yr for workers of some species, such as Aphaenogaster rudis (Emery), for others, such as Solenopsis invicta Buren, it is only 10-70 wk (Hölldobler and Wilson 1990).

Tenebrionidae-Eleodes sp., and F. Cerambycidae—probable Leptura sp.; Table 1).

On the other hand, Windsor (1964) and Henderson and Akre (1986) reported 3 major groups not found in our limited sampling: Arachnida (small spiders), Thysanura (silverfish), and Orthoptera (F. Gryllidae). In addition, Weber (1935), Windsor (1964), and MacKay and MacKay (1984) noted many dipteran and coleopteran families not in our nests and new genera and species in a few of the same families found in our nests (Table 1).

The relationship of these myrmecophiles with the host colony is unclear. Larval and adult coleopterans and noctuid larvae may use the chambers for hibernation or development (Weber 1935). Staphylinid beetles may prey upon brood or workers. Jones (1929) suggested that lepidopteran, coleopteran, and dipteran larvae are tolerated because they feed on decaying vegetable matter in the nest. Cremastocheilus is a well-known symbiont in the nests of a number of ant species (Hölldobler and Wilson 1990). The scarab genus Euphoria may be a symbiont treated with indifference by the host colony (Wheeler 1910). On the other hand, ants are aggressive to other guests, such as the myrmecophilous cricket (Myrmecophila manni Schimmer; Henderson and Akre 1986). Weber (1935) reported 3 ant species in nests (Table 1) and noted that *Leptothorax hirticornis* Emery may prey upon brood or isolated workers. Tapinoma sessile, one of the species in our nests, often steals honeydew from thatching ants throughout its territory, but seems to elicit little defensive response (McIver and Loomis 1993). The high altitude of our study site did not seem to significantly alter nest dimensions and ecology, but the work did provide new findings on this species, such as the greatest mound density per hectare, first report of probable P. maniculatus fecal pellets associated with mound thatch, new information on the thermal properties of mounds, new information on worker longevity, greatest number of wingless queens reported in a nest, and possible new myrmecophiles.

Mites were found on only 3 workers in our study area. Weber (1935), on the other hand, noted that mites (Parasitidae, Tyroglyphidae, Uropoda sp.) were common on workers and sexuals, especially on the tibia-tarsal joint, and estimated over 200 on 1 queen.

Excavated nests varied in depth from 0.3 to 0.97 m, or less than the maximum depth of 1.37 m noted by McCook (1884) and 1.58 m reported by Weber (1935). Weber speculated that the water table (below 1.52 m) limits nest depth.

Nests excavated from 27 June to 6 August did not contain winged reproductives except a male in 1 nest. This finding differs from Cole's (1932) observations of large numbers of winged reproductives through June and July.

Many species of Formica are polygynous (Kannowski 1963). The number of wingless queens per Colorado nest varied from 0 to 198 (Conway 1996). The latter number far exceeds the 2 or more queens per colony reported by Cole (1932).

The following arthropod groups found in our excavated nests had not been reported associated with this species: pseudoscorpions, collembolans (F. Entomobryidae), homopterans (F. Aphididae, F. Cicadellidae), hemipterans (F. Anthocoridae), dipterans (F. Asilidae), and cole-

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