Contributions to Entomology 75 (1) 2025, 229–233 | DOI 10.3897/contrib.entomol.75.e144856

CONTRIBUTIONS
TO ENTOMOLOGY

SENCKENBERG

Research Article

Overwintering by the western thatch ant, *Formica obscuripes* (Hymenoptera, Formicidae)

D. Christian Furness[1], Elaine Tan[1], John T. Longino[1]

1 *School of Biological Sciences, University of Utah, Salt Lake City, UT 84112, USA*

https://zoobank.org/407829A6-A185-4173-932D-61373F730A40

Corresponding author: D. Christian Furness (cfurness0@gmail.com)

Academic editor: Stephan M. Blank | Received 13 January 2025 | Accepted 20 April 2025 | Published 28 May 2025

Abstract

Temperate zone ants overwinter using a variety of mechanisms. The genus *Formica* overwinters entirely as adults. In at least one species it has been demonstrated that winter workers are more corpulent than summer foragers, storing resources in their bodies and mobilizing them for early brood production in spring. Here we examine overwintering by the common western thatch ant, *F. obscuripes*. Excavation of a winter nest revealed only workers, distributed in multiple chambers in a roughly spherical region from 0.5 to 1.05 m deep. Worker size, as measured by head width, was weakly bimodal, with fewer workers in the small vs. large size class. We measured dry weights of workers from the winter nest and workers collected the previous summer from the surfaces of multiple nests in the vicinity, including our excavated nest. Controlling for size, there was no evidence of bimodality in winter worker weight, and winter workers were 59.7% heavier than summer foragers. These results suggest that *F. obscuripes* workers are at their maximum corpulence going into their first winter, expend their stored fat during spring, and mostly die before overwintering a second time. It remains uncertain whether workers can regain corpulence.

Key Words

Overwintering, seasonal adaptation, worker corpulence

Introduction

Insects encounter annual variation in abiotic conditions that influence important life events both physically and physiologically (Chown and Nicolson 2004). In the case of insects that live in the temperate zone, one of these significant abiotic conditions is seasonal changes and the need to successfully overwinter by retreating from the cold to avoid cold exposure (Sinclair 2014; Sunday et al. 2014). Winter months for insects have proven to be a time of food shortage (Leather et al. 1995) and high mortality for some species (Leather 1993). One physiological mechanism used to overcome these challenges while overwintering is the storage and use of lipids (Lease and Wolf 2010).

Ants (family Formicidae) have long-lived adults that in the temperate zone require mechanisms to overwinter (Kipyatkov 2001). Temperate zone ants, like many other insects, overwinter below ground to avoid low winter temperatures (e.g., Kondoh 1968a; Włodarczyk 2020) . It is an effective strategy, but this can also delay spring emergence (Włodarczyk 2020).

Another mechanism that can aid overwintering ants is lipid storage. Seasonal lipid fluctuation has been studied in *Formica japonica*, *Solenopsis invicta*, *Pogonomyrmex barbatus*, and *P. badius* (Kondoh 1968b; Tschinkel 1993, 1998; Roeder et al. 2023). *Pogonomyrmex badius* has a large pulse of early-spring sexuals that cannot be produced solely from current foraging intake. The metabolic and labor resources needed for sexual production are stored in the bodies of the young workers, whose fat content reaches the annual minimum after producing sexuals. After these sexuals have flown, the colony once again switches to producing workers and storing excess foraging intake as worker fat for over-wintering, and for producing the next year's sexuals (Tschinkel 1998). *Pogonomyrmex barbatus* was shown to have patterns of dry weight similar to those of *P. badius*, with a low in the summer and high in the winter months (Roeder et al. 2023). *Formica japonica* has heavier workers in the winter and a bimodality of corpulent and lean workers (Kondoh 1968b). *Formica japonica* workers emerge as adults with an intermediate corpulence level before gaining more fat prior to overwintering (Kondoh 1969).

In the genus *Formica*, egg production is not continuous throughout the year. Egg production stops in mid to late summer so that when winter arrives, they have no larvae, pupae, or eggs to care for, and colonies will only contain worker ants and one or more queens (Eidmann 1943; Hasegawa and Yamaguchi 1994). They overwinter underground and then immediately in spring, following snow melt, eggs are produced once again. Workers begin to rear a cohort of sexual brood before any significant foraging commences (Lopatina 2018). During spring there is presumably a transition from use of stored food resources to new food obtained from foraging, with a premium on acquiring food as early as possible. For example, in *Formica polyctena* (wood ants), workers not only fight for territory in the spring but also capture and kill opposing colony workers that they feed to the queen and sexual larvae, accelerating the production of sexuals (Mabelis 1984).

Formica obscuripes, the western thatch ant, is a successful ant species present in a variety of habitats of the western United States, at elevations from 1500–2500 m (Wheeler 1913; Cole 1932). They use twigs and dry plant material to create dome-shaped thatch mounds. Workers are very active on the mound surface from early spring to late summer, but then disappear below ground during winter. Winter conditions of *F. obscuripes*' nests have not been investigated. We investigated the natural history of overwintering *F. obscuripes* by excavating a nest in winter and examining the distribution and abundance of workers in chambers. We obtained head widths and dry weights of workers to examine whether workers showed the bimodality observed in *F. japonica* by Kondoh (1968b). We also obtained sizes and weights of workers on the surfaces of multiple mounds during the summer prior to excavation. We predicted that winter workers would be heavier than the summer foragers due to the additional stored fat for overwintering.

Methods

Field site and sampling methodology

Fieldwork was carried out in the Wasatch Range portion of the greater Rocky Mountains in the arid western United States, in the same area described in Tan (2023). Data was collected in Big Cottonwood Canyon, in a 4 km^2 area between 2400 to 2750 m elevation in the southeastern portion of the Wasatch Range's extension through Salt Lake County, Utah (Fig. 1). Average annual temperature in Big Cottonwood Canyon is 2.0 °C, and average annual precipitation is 751 mm, but there is a large difference in temperature and precipitation conditions between the winter (dormant) season from October to May (average temperature in January is -8.9 °C) and the summer (growing/active) season from June to

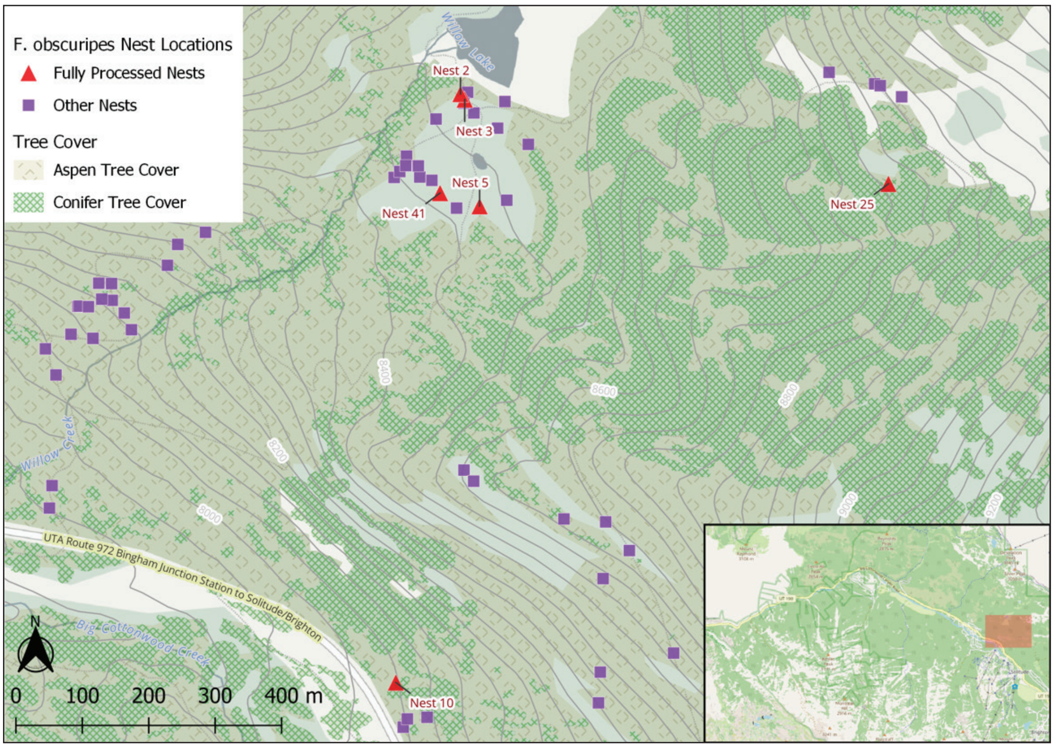

Figure 1. Sampling site of *Formica obscuripes* nests in Big Cottonwood Canyon, Utah.

September (average temperature in July is 17.1 °C). The study site comprises mixed aspen-conifer forest with predominantly aspen (*Populus tremuloides*) and white fir (*Abies concolor*). Ant nests were found in open areas (scrub/meadow), at the edges of aspen forest, or in mixed aspen-conifer forest. Nests were discovered by searching a rough grid pattern every 20 meters over several spots bordering open areas in each quadrant of the 4 square kilometers, looking for fallen logs with thatch, large rocks surrounded by thatch, and thatch mounds.

Winter collection

A thatch mound nest that had been observed through the summer was selected for winter excavation. During multiple visits between 19 November and 16 December 2022, most of the nest was excavated. A 1.05 m deep pit was dug to the side of the nest, and then excavation proceeded by carving sections of soil away and mapping chambers as they were encountered, using an x,y,z coordinate system. The soil was filled with rocks and boulders, which were carefully pried away to reveal any chambers. The upper 35 cm was a dark organic horizon, below which was hard-packed lighter mineral soil, requiring a pickaxe to excavate. On encountering a chamber it was numbered and the workers scooped out and placed in a plastic bag. Temperatures of surfaces and chambers were recorded with an infrared thermometer. We excavated about two thirds of the volume beneath the surface mound, including the area beneath the apex. Chamber contents were transported to the lab and stored in a 6 °C refrigerator. The number of ants in each chamber was recorded. Twenty individuals were haphazardly selected from each chamber for weighing and measuring. If the chamber contained fewer than 20 workers, all individuals were used. Dry weight (DW) was obtained by first freezing workers to kill them, placing them in individual 1 ml vials in a heating table at 56 °C for 24 hours, and then weighing them on an analytical scale. Weights were to the nearest 0.01 mg. Maximum head width (HW) in face view was measured to the nearest 0.01 mm, using a dissecting microscope and a micrometer stage.

Summer collection

In summer 2022, prior to the winter excavation, we located six colonies with active mounds, within 1.05 km of each other. Following snow-melt, colonies were visited weekly. A sample of ten workers was taken from the surface of each mound. Workers were selected haphazardly, attempting to minimize size bias. Workers were collected during midday when they were active. Workers were stored on ice in a cooler for return to the lab. In the lab individual workers were placed in separate 1 ml vials and frozen in a -20 °C freezer. After 24 hours they were dried, weighed, and measured as described for the winter excavation.

Analysis

An exponential relationship between HW and DW is expected, with the exponent being influenced by scaling (with DW being related to volume) and allometry (with HW increasing disproportionately in larger workers). DW was log transformed for all analyses, to achieve linear relationships between HW and log(DW). A Hartigan dip test (Hartigan and Hartigan 1985) was used to test for bimodality of worker head size for the excavated nest. The relationship of HW and log(DW) to depth was examined with linear regression. Heterogeneity of HW and log(DW) among chambers was tested with ANOVA. To test for differences in log(DW) between winter and summer workers, we used ANCOVA, with HW as the continuous independent variable and season (winter or summer) as a cofactor. In the winter nest, we tested whether worker corpulence was bimodal, separating into lean and corpulent subpopulations. We applied a Hartigan dip test to the residuals of the HW × log(DW) regression.

Results

Across the three days of the winter nest excavation there was variation in surface ground temperature from –1 to –13 °C. The temperature of the chambers varied from –2 to 5 °C.

During excavation we encountered 27 chambers. The chambers contained workers only, with no brood and no evidence of any stored food. Three individual workers were encountered in a tunnel at 30 cm depth; these were excluded from any further analysis. The first chamber encountered was 45 cm deep. Chambers varied greatly in shape and size. Some chambers were pancake-shaped, some were more cylindrical, while others were irregular and appeared opportunistically formed along rocks or roots. Chambers were found at 105 cm depth, but tunnels continued deeper, suggesting more of the colony remained at greater depth. No queen was found, suggesting the queen might have remained in a deeper chamber. In a previous excavation of a different nest we found a dealate queen in the deepest chamber of the nest, at 150 cm depth. No larvae or pupae were found. The chambers were scattered in a general spherical volume. In total, 4,417 workers were collected. The least populated chamber contained 13 workers and the most populated chamber contained 579 workers. The average chamber population was 170 ants. The distribution of workers with respect to depth shows the greatest density at an intermediate depth, 70–80 cm (Fig. 2).

The over-wintering colony workers had a head width that trended towards bimodality but the dip test was not significant ($p = 0.0525$) (Fig. 3). There was no evidence of spatial segregation of workers by HW or log(DW) in the colony. There was no relationship of worker size or dry weight to depth (HW: $r^2 = 0.0004$, $p = 0.64$; log(DW): $r^2 = 0.001$, $p = 0.43$). There was also no relationship of worker dry weight to chamber (ANOVA log(DW): $F(25, 486) = 1.521$, $p = 0.05213$). There was however a slight relationship between worker size to chamber (ANOVA HW: F(25,

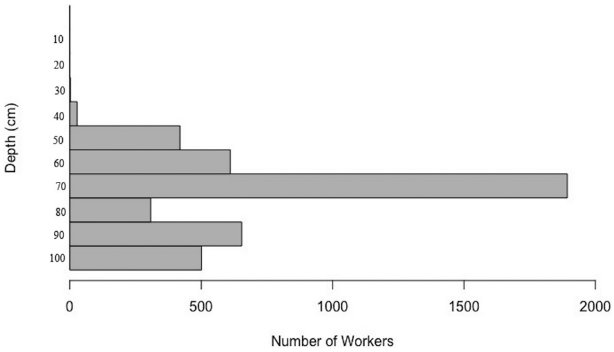

Figure 2. Distribution of *Formica obscuripes* workers with respect to depth in an over-wintering colony. The distribution may be truncated, with an unexcavated portion of the colony below 110 cm.

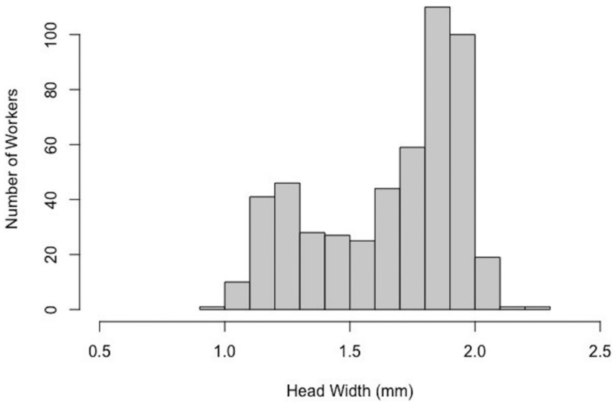

Figure 3. Distribution of *Formica obscuripes* worker head width in an over-wintering colony. Workers show a trend toward bimodality.

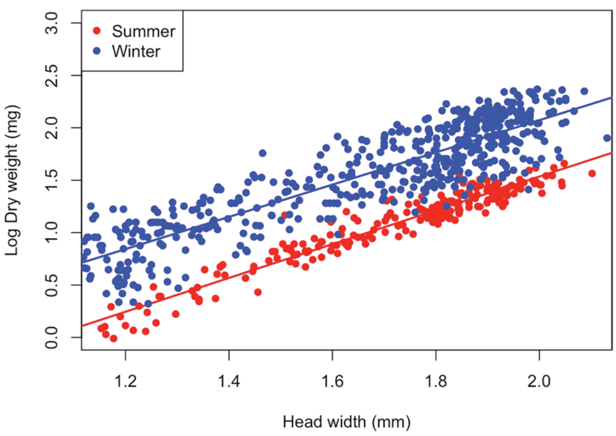

Figure 4. Relationship of dry weight to head width of *Formica obscuripes* workers, comparing summer foragers to workers in an over-wintering colony.

486) = 1.642, $p = 0.02692$, $r^2 = 0.03$). This relationship does not appear strong though as the lowest median size of a chamber was 1.595 mm with the largest being 1.929 mm. The residuals of the HW × log(DW) regression showed no signs of bimodality and had a roughly normal distribution.

Workers in the over-wintering colony were heavier than the summer-collected workers (Fig. 4) (ANCOVA: $F(1, 728) = 1407$, $p < 0.001$). The average dry weight of the summer and winter workers was 3.3 mg and 5.27 mg, respectively. The winter workers were 59.7% heavier than the summer foragers.

Discussion

In our winter excavation no external food sources, eggs, larvae, or pupae were found in the chambers. A similar lack of stored food or brood was found in an exploratory excavation of another nest in 2020. This confirms the observation in other *Formica* species that they over-winter without brood or any externally stored food resources. Based on our excavated colony, *F. obscuripes* appears to share many similarities with *F. japonica*. *Formica obscuripes* and *F. japonica* had a similar distribution of workers in the nest, with a greater proportion at intermediate depths (Kondoh 1968a). Although not as obvious as the HW bimodality of *F. japonica*, we also saw trends of HW bimodality in our *F. obscuripes* nest.

We found that the dry weight of winter workers was much greater than the dry weight of summer foragers. Several mechanisms could explain this. If worker corpulence can fluctuate, increasing or decreasing rapidly, the difference could be due to temperature dependence of metabolism (Shik et al. 2019). Summer foragers may have less lipid content as their social roles require more exposure to higher temperatures and more energy consumption as they forage outside of their thatch mounds. Temperature has been shown to be a possible factor in ant lipid content fluctuation for *Pogonomyrmex barbatus* (Roeder et al. 2023).

Alternatively, new workers may eclose with maximum corpulence, expend it in the spring and summer, and then never regain it. In the typical progression of temporal polyethism, workers may emerge in their first summer, engage entirely in brood care or nest maintenance until they overwinter, divest their lipid stores in spring, and then become external foragers. Our summer workers from nest surfaces were probably a biased sample of the entire nest population, consisting largely of these workers near the end of their lives. Kondoh (1969) observed two separate classes of summer workers in *F. japonica*, one consisting of newly emerged workers that stayed in the nest and were more corpulent, the other consisting of foragers which were leaner. We did not observe any bimodality of corpulence in the winter nest, which suggests that few of the foraging workers survive to overwinter a second time. Longevity of foraging workers is known to be very short (Porter and Jorgensen 1981; Schmid-Hempel and Schmid-Hempel 1984; Gordon and Hölldobler 1987; Conway 1996). If there are older foragers in the overwintering population, it is likely that they represent a very small fraction of the overall population. It remains unknown whether lean workers can ever regain corpulence.

A better understanding of how corpulence changes and functions through the seasons in ants is important in this time of rapid climate change and warming. Corpulence dynamics may be a major contributor to ant colony phenology and mortality as summers become warmer and winters shorter.

Acknowledgements

We would like to thank all those who provided feedback and reviewed this manuscript. We want to thank the University of Utah's Office of Undergraduate Research for their Undergraduate Research Opportunity Program for funding this work.

References

Chown SL, Nicolson SW (2004) Insect physiological ecology: Mechanisms and patterns. Oxford University Press, Oxford, 243 pp. https://doi.org/10.1093/acprof:oso/9780198515494.001.0001

Cole AC (1932) The Thatching Ant, *Formica obscuripes* Forel. Psyche: A Journal of Entomology 39(1–2): 30–33. https://doi.org/10.1155/1932/61715

Conway JR (1996) A field study of the nesting ecology of the thatching ant, *Formica obscuripes* Forel, at high altitude in Colorado. Great Basin Naturalist 56: 326–332.

Eidmann H (1943) Die Überwinterung der Ameisen. Zeitschrift für Morphologie und Ökologie der Tiere 39(2): 217–275. https://doi.org/10.1007/BF00684467

Gordon DM, Hölldobler B (1987) Worker longevity in harvester ants (*Pogonomyrmex*). Psyche: A Journal of Entomology 94: 341–346. https://doi.org/10.1155/1987/63930

Hartigan JA, Hartigan PM (1985) The dip test of unimodality. The Annals of Statistics 13: 70–84. https://doi.org/10.1214/aos/1176346577

Hasegawa E, Yamaguchi T (1994) Raiding behavior of the Japanese slave-making ant *Polyergus samurai*. Insectes Sociaux 41: 279–289. https://doi.org/10.1007/BF01242299

Kipyatkov VE (2001) Seasonal life cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea). Acta Societatis Zoologicae Bohemicae 65: 211–238.

Kondoh M (1968a) Bioeconomic studies on the colony of an ant species, *Formica japonica* Motschulsky 1. Nest structure and seasonal change of the colony members. The Ecological Society of Japan 18: 124–133.

Kondoh M (1968b) Bioeconomic studies on the colony of an ant species, *Formica japonica* Motschulsky 2. Allometric study of the body weight and the corpulency relating to the body size of workers. The Ecological Society of Japan 18: 171–179.

Kondoh M (1969) Bioeconomic studies on the colony of ant species, *Formica japonica* Motschulsky 3. Body weight of the workers at the emergence from the cocoons. The Ecological Society of Japan 19: 8–12.

Lease HM, Wolf BO (2010) Lipid content of terrestrial arthropods in relation to body size, phylogeny, ontogeny and sex. Physiological Entomology 36: 29–38. https://doi.org/10.1111/j.1365-3032.2010.00767.x

Leather SR (1993) Overwintering in six arable aphid pests: A review with particular relevance to Pest Management. Journal of Applied Entomology 116: 217–233. https://doi.org/10.1111/j.1439-0418.1993.tb01192.x

Leather SR, Walters KA, Bale JS (1995) The Ecology of Insect Overwintering. Cambridge University, Cambridge, 268 pp.

Lopatina EB (2018) Structure, diversity and adaptive traits of seasonal cycles and strategies in ants. In: Shields VDC The Complex World of Ants. IntechOpen, London, 7–49. https://doi.org/10.5772/intechopen.75388

Mabelis A (1984) Aggression in Wood Ants (*Formica polyctena* Foerst., Hymenoptera, Formicidae). Aggressive Behavior 10: 47–53. https://doi.org/10.1002/1098-2337(1984)10:1%3C47::AID-AB2480100107%3E3.0.CO;2-N

Porter SD, Jorgensen CD (1981) Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste? Behavioral Ecology and Sociobiology 9: 247–256. https://doi.org/10.1007/BF00299879

Roeder DV, Remy S, Roeder KA (2023) Temperature influences lipid content in the red harvester ant, *Pogonomyrmex barbatus*. Journal of Insect Science 23(3): 1–5. https://doi.org/10.1093/jisesa/iead040

Schmid-Hempel P, Schmid-Hempel R (1984) Life duration and turnover of foragers in the ant *Cataglyphis bicolor*. Insectes Sociaux 31: 345–360. https://doi.org/10.1007/BF02223652

Shik JZ, Arnan X, Oms CS, Cerdá X, Boulay R (2019) Evidence for locally adaptive metabolic rates among ant populations along an elevational gradient. Journal of Animal Ecology 88: 1240–1249. https://doi.org/10.1111/1365-2656.13007

Sinclair BJ (2014) Linking energetics and overwintering in temperate insects. Journal of Thermal Biology 54: 5–11. https://doi.org/10.1016/j.jtherbio.2014.07.007

Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proceedings of the National Academy of Sciences 111: 5610–5615. https://doi.org/10.1073/pnas.1316145111

Tan EN (2023) Colony Founding Biology in a Genus of Temperate Social Parasite Ants with a Focus on the Western Thatching Ant *Formica obscuripes*. Masters Thesis, University of Utah, Salt Lake City, United States of America. https://www.proquest.com/docview/2877266577

Tschinkel WR (1993) Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. Ecological Monographs 63: 425–457. https://doi.org/10.2307/2937154

Tschinkel WR (1998) Sociometry and sociogenesis of colonies of the Harvester Ant, *Pogonomyrmex badius*: Worker characteristics in relation to colony size and season. Insectes Sociaux 45: 385–410. https://doi.org/10.1007/s000400050097

Wheeler WM (1913) A revision of the ants of the genus *Formica* (Linné) Mayr. Bulletin of the Museum of Comparative Zoology 53: 379–565.

Włodarczyk T (2020) Functional spatial distribution and sociometric characteristics of *Formica fusca* ants during winter dormancy. Ecological Entomology 46: 419–427. https://doi.org/10.1111/een.12983

Supplementary material 1

Ant measurement data

Authors: D. Christian Furness, Elaine Tan, John T. Longino
Data type: xlsx
Explanation note: This data contains weight measurements of individual ants, their measured headwidth, and the winter nest excavation data.

Link: https://doi.org/10.3897/contrib.entomol.75.e144856.suppl1