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USE OF A SECONDARY NEST IN GREAT BASIN DESERT THATCH ANTS (*FORMICA OBSCURIPES* FOREL)

James D. McIver¹ and Trygve Steen²

ABSTRACT.—Workers of Great Basin Desert thatch ants (*Formica obscuripes* Forel) dig simple secondary nests at the base of plants upon which they tend aphids and scales. These secondary nests house only foragers, with the number of foragers occupying each nest positively correlated with the number of worker-tended Homoptera feeding on plant foliage above. Thatch ant secondary nests are cooler than 25 cm below the dome top of the primary nest and maintain a significantly more constant temperature than is observed on the ground surface or in the plant canopy. Thatch ant foragers use secondary nests for at least two purposes: as a cool refuge for Homoptera tenders when midday plant canopy temperatures rise during the summer months, and as the primary place within which Homoptera tenders transfer honeydew to larger “honeydew transporters” for ultimate transport back to the primary nest.

Key words: honeydew harvest, thermal refugia, behavioral thermoregulation, red wood ants, desert adaptation, satellite nests.

Although most ant species use a nest structure consisting of a single central location (a primary nest), many species also employ “secondary” nests in which a portion of the colony population is dispersed among several alternate sites (Wheeler 1910).

Several species of *Camponotus*, for example, use a secondary nest to which workers transport late-instar larvae and pupae from a central location occupied by the queen and brood (Hansen and Akre 1987). Similarly, the dolichoderine *Iridomyrmex sanguineus* maintains secondary nests containing older larvae and pupae, but workers bring young from several locations within oligogynous colonies (McIver 1991).

Many other ant species (*Polyrachis simplex*, *Lasius niger*, *L. emarginatus*, *Formica pratensis*, *F. exsectoides*, *Crematogaster pilosus*) are known to use secondary nests in which only foraging workers reside (Forel 1921, Andrews 1929, Ofer 1970). These secondary nests are thought to serve as refuges for the workers from the physical environment, as a defense against enemies, or as a protected site within which to tend Homoptera for honeydew (Wheeler 1910).

This paper characterizes the secondary nest used by the thatch ant *Formica obscuripes* Forel living in the Great Basin Desert and discusses its possible function within the context of the desert environment.

STUDY AREA AND SPECIES

Thatch ants were studied between June 1987 and September 1991 at Pike Creek, 160 km southeast of Burns, Oregon. The Pike Creek study site is at 1300 m elevation at the base of Steen’s Mountain in the northern Great Basin Desert. Sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), horsebrush (*Tetradymia* sp.), lupine (*Lupinus caudatus* Kellogg), and cheatgrass (*Bromus* spp.) are dominant plants at the site, which was grazed moderately by cattle throughout the study period.

A total of four colonies of *Formica obscuripes* Forel were observed for various parts of the study. *F. obscuripes* is a widespread and abundant North American *rufa*-group species (Wheeler and Wheeler 1983). Like *F. rufa*-group species elsewhere, *F. obscuripes* builds symmetrical, dome-shaped primary nests of thatch, from which radiate trunk trails that access foraging territory. In all four study colonies workers foraged for honeydew on sagebrush, rabbitbrush, horsebrush, and/or lupine, and scavenged for arthropods in the area surrounding each nest. Although broodless satellite nests were occasionally observed, there was no evidence of primary nest polydomy in any study colonies.

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METHODS AND MATERIALS

Secondary Nest Characteristics

The aboveground structure of the secondary nest is portrayed by a photograph taken from colony 5 at Pike Creek, August 1988. The belowground structure was investigated by pouring a measured quantity of dental labstone down 10 different secondary nest entrances of two colonies (colonies 4 and 26) during August 1991. Quantity of labstone required to fill each secondary nest was then correlated with basal plant diameter and number of workers tending Homoptera in the plant canopy. Actual structure of the secondary nest interior was determined by excavating two nests, photographing the labstone "plug" in place, and drawing one of these to scale using the photograph as reference.

Temperature at 6 cm depth in a typical secondary nest (plant A, colony 2) was measured during summer 1987 and compared to measurements for tending localities in the plant canopy, ground surface, and 25 cm below the top of the primary nest dome.

Secondary Nest Use

Use of the secondary nest by thatch ant workers was explored by conducting intensive observations on a selected sagebrush plant (plant 13) at the Pike Creek study site during July 1987. Beginning 1 July 1987, thatch ants working in the vicinity of plant 13 were individually marked with "beenumbers" (Charles Graz Co., Frankfurt, Germany) so that the activity pattern of each could be determined. By 23 July, a total of 66 workers had visited plant 13 and been marked, 30 of which were still using the plant daily. At noon on 23 July, we began a 24-h continuous period of observation of worker behavior on plant 13. We recorded the location and task of each worker at 15-min intervals throughout the 24-h period and noted its interaction with other workers. The result was a time budget for 30 different workers that frequented plant 13 during the 24-h period, from which we could infer how workers of various task specializations used the secondary nest at the plant base.

RESULTS

Secondary Nest Characteristics

Thatch ant secondary nests were found at the base of each plant upon which workers

tended Homoptera at Pike Creek during the study period. Viewed from above, secondary nests were simple openings in the ground adjacent to plant trunks (Fig. 1). Ground around an opening was typically littered with thatch material, fallen from the plant canopy, blown in, or excavated from the gallery beneath.

Volume of 10 secondary nests beneath active tending groups of workers ranged from 35 to 125 cc. Secondary nest volume was not significantly correlated with basal plant diameter ($R^2 = .02$, $P > .05$, $N = 10$) but was significantly correlated with number of tenders ($R^2 = .33$, $P < .05$, $Y = .54X + 43.3$, $N = 10$).

Excavations of secondary nests into which labstone had been poured revealed that cavities essentially conformed to morphology of the plant trunk itself (Fig. 2). Thatch ant workers typically removed dirt, small stones, and other debris from within 5–20 mm of the plant trunk, leaving a cavity punctuated with large stones and roots. The nest represented in Figure 2 was 10.8 cm deep and consisted of three separate chambers totaling 175 cc in volume.

Temperature within the secondary nest differed considerably from temperatures recorded simultaneously on the ground surface, in the plant canopy, or deep within the primary nest (Fig. 3). Over the 1-wk period 13–19 June 1987, for example, the secondary nest we measured was an average of about 7°C cooler than 25 cm from the dome top of the primary nest (18.8° vs. 26.1°), with a little over twice the variance over time (12.6 vs. 5.7). Compared to ground surface, the secondary nest was slightly cooler (18.8° vs. 19.2°) but much less variable, exhibiting a variance of about one-ninth the ground surface (12.6 vs. 112.4). Compared to the canopy of the same plant, the secondary nest was slightly warmer on average (18.8° vs. 18.0°) but about one-fifth as variable (12.6 vs. 67.1). Temperature trends over the entire summer were similar to those measured in this 1-wk sample period in mid-June.

Secondary Nest Use

Observations of individually marked workers on plant 13 of colony 2 clearly show that the secondary nest is used throughout the day (Fig. 4). The greatest percentage of workers was found in the secondary nest during mid-afternoon, corresponding to highest daily tem-

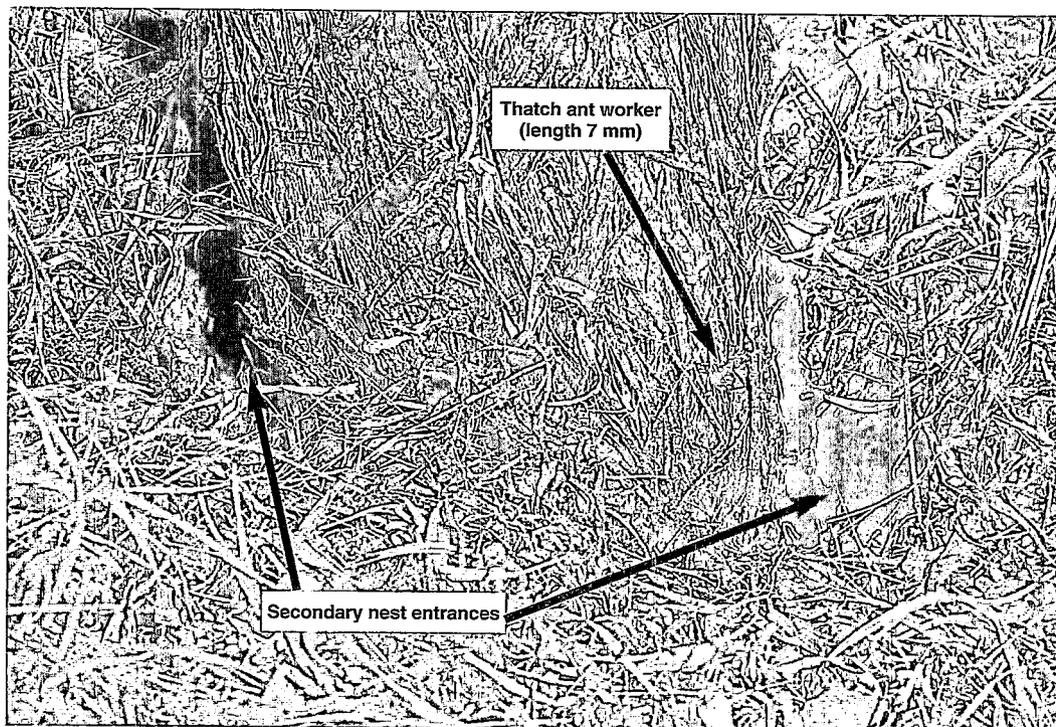


Fig. 1. Aboveground appearance of secondary nest at base of sagebrush plant, Pike Creek, southeastern Oregon, June 1994 (photograph by Trygve Steen).

peratures. Secondary nest population was lowest between 1700 and 2000, and between 0600 and 0900, during principal times when workers deliver honeydew to the primary nest.

Two typical patterns of activity were observed for plant-associated workers (Fig. 5). **Tenders** spent the majority of their time tending Homoptera for honeydew in the plant canopy. Worker 84, for example, spent 54% of her time tending aphids, with each visit to the plant canopy lasting between 2 min and about 3 h. Her visits to the plant canopy were interspersed with frequent visits to the secondary nest at the plant base, where it is likely she transferred honeydew to larger nontending individuals like worker 13 (chain transport). Twice per day she returned to the primary nest: once in the early evening and once in the morning.

Honeydew transporters spend the majority of their time in the secondary nest itself. Worker 13, for example, spent 66% of her time in the secondary nest, 23% scavenging on the ground surface, and 9% on twice-daily returns to the primary nest. On her returns to the pri-

mary nest, worker 13 often had a distended gaster, indicating a crop swollen with honeydew. Typically, workers like #13 were scavengers, secondary nest excavators, and/or honeydew transporters, receiving the majority of their honeydew from workers that concentrated on tending Homoptera in the plant canopy.

Of the 30 workers associated with plant 13 during the intensive observation period, 19 were classified as tenders, 6 as honeydew transporters/scavengers, 2 had behavior intermediate between tender and transporter/scavenger, and 3 were not observed often enough to classify.

DISCUSSION

Great Basin Desert thatch ants use secondary nests as a refuge from high midday temperatures and as a site within which honeydew is transferred from workers who collect it in the plant canopy to those who help transport it back to the primary nest. Ground temperatures above 50°C have been reported as lethal to *F. obscuripes* (O'Neill and Kemp 1990), and Mackay and Mackay (1984)

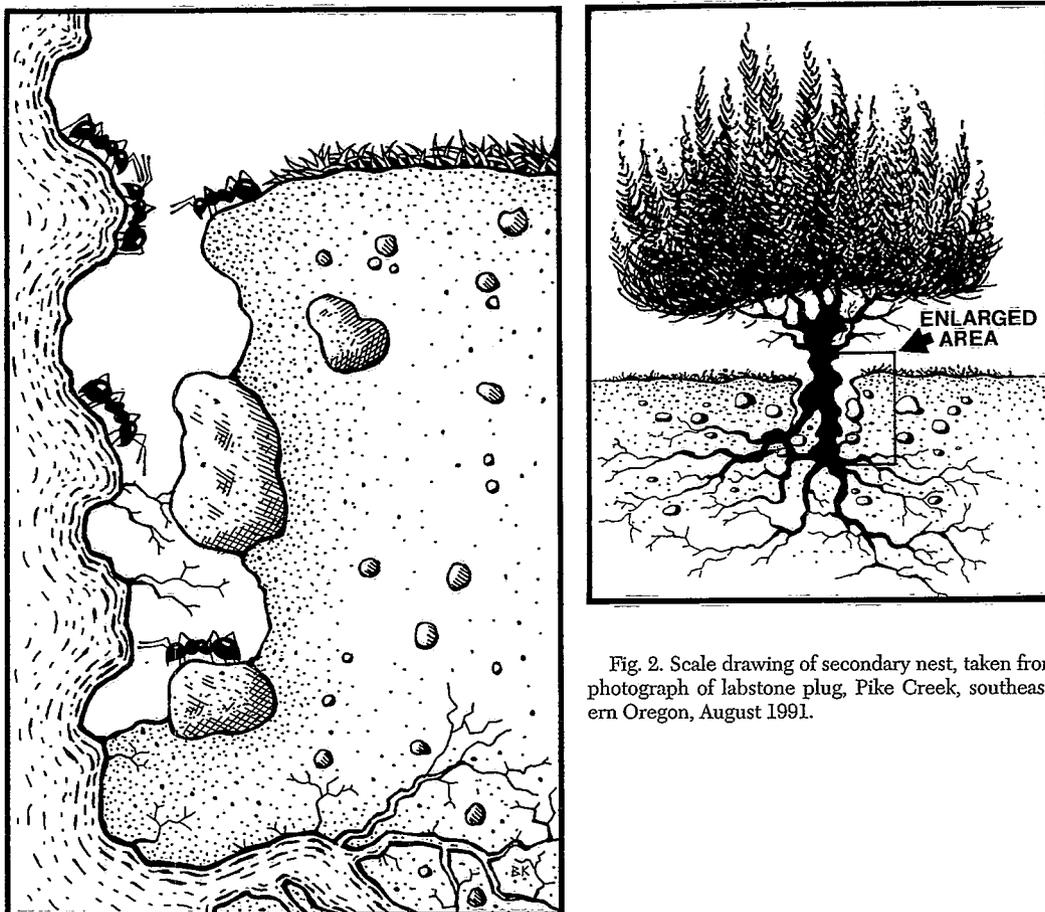


Fig. 2. Scale drawing of secondary nest, taken from photograph of labstone plug, Pike Creek, southeastern Oregon, August 1991.

observed that *F. haemorrhoidalis* workers hide under pine cones or retreat to shady places during midday heat. Chain transport appears to be an effective way to increase delivery of honeydew to the primary nest (McIver and Yandell 1994); thus, it is not surprising that honeydew transfer occurs at a site offering refuge from midday heat.

The use of cool midday refugia by workers may also reduce metabolic costs and increase worker longevity. In a study on fire ant thermal preferences, Porter and Tschinkel (1993) reported that fire ant workers consistently choose cooler temperatures than those selected for the brood. They postulate that this tendency increases longevity of workers not directly associated with brood care. This idea is supported by Calabi and Porter (1989), who demonstrated that because temperature and metabolic rate are highly correlated, fire ants reared and maintained under high temperature regimes have lower longevity.

Thatch ants living at other sites in the Great Basin also use secondary nests of this kind (McIver personal observation); Weber (1935) described secondary nests in his study of South Dakota thatch ants. However, Weber reported that the function of these nests was to serve as (1) an arborescent chamber within which to tend Homoptera and (2) a potential site for development into primary nests. Certainly, colonies of *Formica rufa*-group species often reproduce by budding (Mabelis 1979; *F. polycytena*), and the site of a new primary nest is very often a secondary nest (Scherba 1959, McIver personal observation). It is not known whether *F. rufa*-group species living in other habitats employ secondary nests for these or other reasons.

Other *Formica* species are also known to employ secondary nests. The mound-building ant *F. exsectoides* (*exsectoides*-group) uses secondary nests as shelters for treehoppers and as sites for food exchange (Andrews 1929).

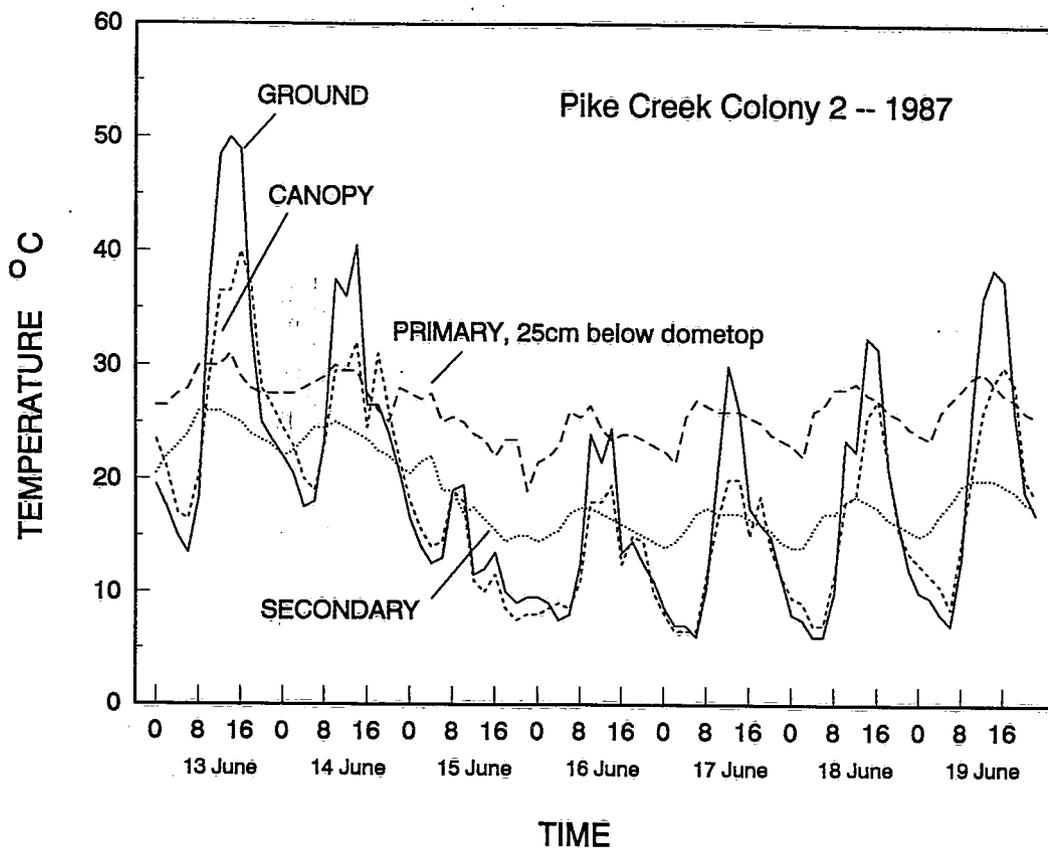


Fig. 3. Temperature ($^{\circ}\text{C}$) during week of 13–19 June 1987, on ground surface, in sagebrush canopy, 25 cm below dome top of primary nest, and in secondary nest of colony 2, Pike Creek, Oregon.

Formica integra of North America and *F. pratensis* of Europe construct secondary nests along covered paths (Wheeler 1910, Forel 1921).

Other Homoptera-tending ants, including the formicines *Lasius niger* (Forel 1921), *L. emarginatus* (Forel 1921), *L. flavus* (Soulie 1961), and *Polyrachis simplex* (Ofer 1970), and the myrmicines *Crematogaster pilosus* (Forel 1921) and *C. auberti* (Soulie 1961), use secondary nests as shelters for their homopteran symbiotes.

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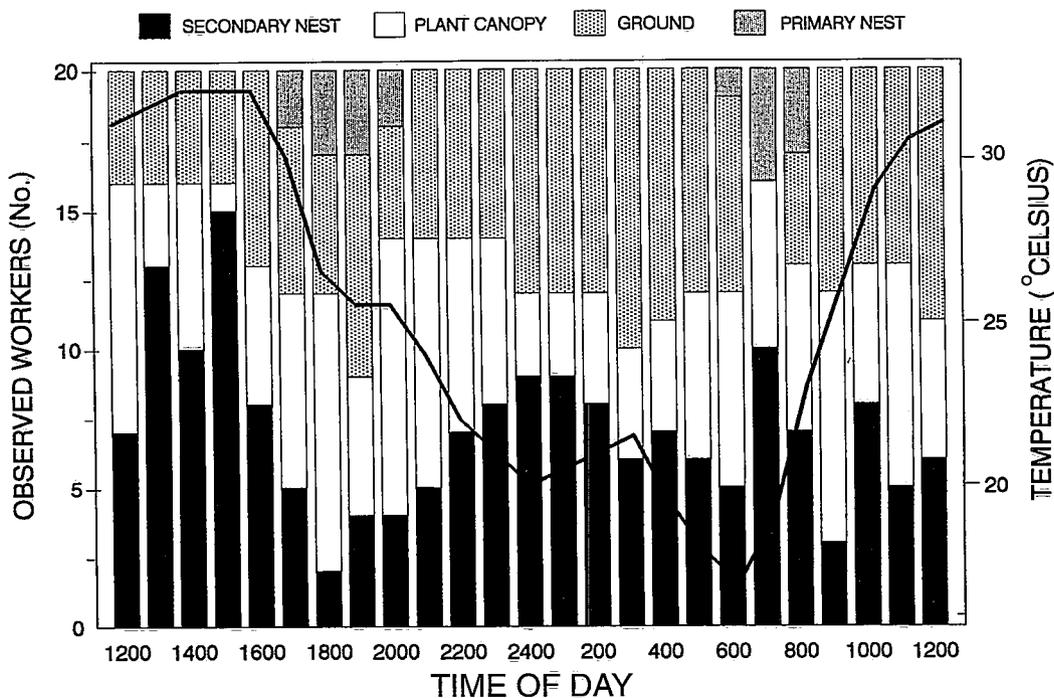


Fig. 4. Activity of marked workers of plant 13, Pike Creek colony 2, 23-24 July 1987. Number of workers observed in secondary nest, in plant canopy, on ground, at primary nest, and temperature in degrees Celsius over 24-h period.

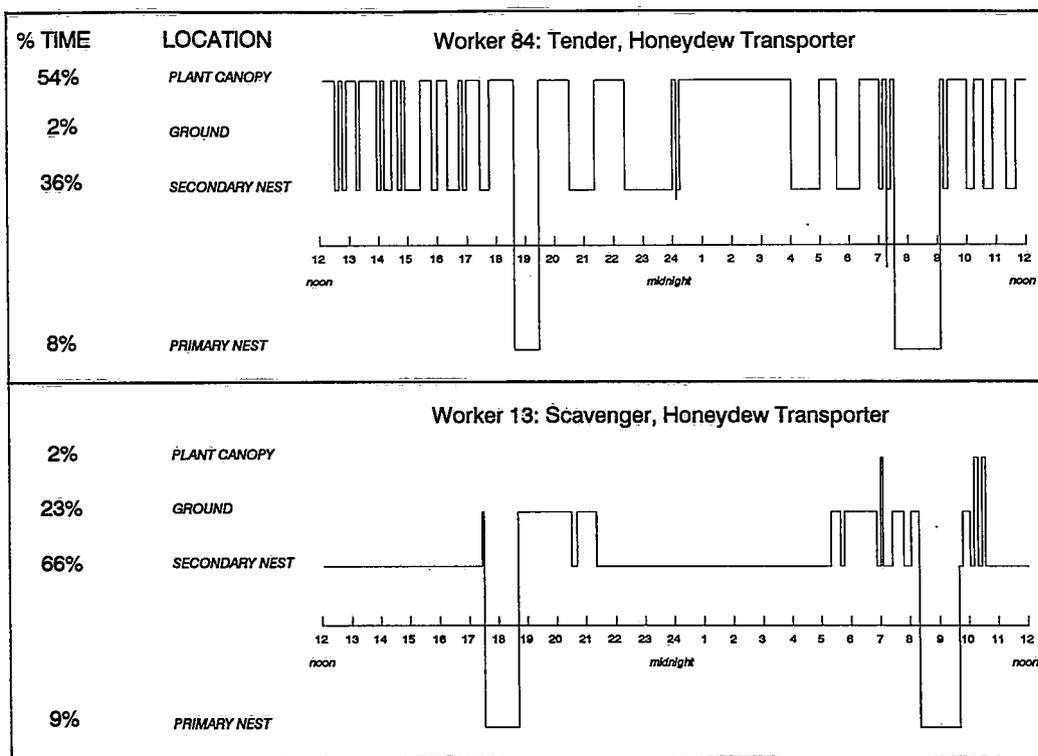


Fig. 5. Activity over 24-h period of workers 84 and 13 on plant 13, colony 2, Pike Creek, Oregon, 23-24 July 1987.

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