Honeydew Harvest in the Western Thatching Ant (Hymenoptera: Formicidae)

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ABSTRACT   Honeydew is a critical resource for colonies of the western thatching ant *(Formica obscuripes* Forel) living in shrub-steppe habitat of the Great Basin Desert. Workers of this ant collect and deliver honeydew to their primary nest in a highly organized way. Honeydew collectors (tenders) show complete fidelity to a single plant and to a distinct group of aphids throughout their foraging lives. At night and during the heat of the day, tenders split their time between tending and making frequent trips to a secondary nest at the plant base, where they transfer some of their honeydew to larger workers (transporters) for ultimate transport back to the primary nest. Both tenders and transporters deliver honeydew at least twice per day along well-established trunk trails, once in the morning and once in the late afternoon, when it is both cool and light. This same foraging pattern occurs each warm day as the summer progresses, with the identity of tenders gradually changing as old workers are replaced by new workers formerly engaged in duties in the interior or on the surface of the primary nest. This highly organized harvesting system underscores the importance of honeydew for nutrition and for territorial defense in the western thatching ant.

FORAGING FOR HONEYDEW IS WIDESPREAD IN ANTS, PARTICULARLY IN the subfamilies Dolichoderinae and Formicinae, species of which have a distensible crop for transport and storage of liquid food (Hölldobler and Wilson 1990). Honeydew is obtained most often from various species of Homoptera (aphids, scales, membracids), but other herbivorous insects, including lycaenid butterfly larvae (Pierce 1987) and several species of Heteroptera, also produce it (Maschwitz et al. 1987). In Homoptera, carbohydrate-rich honeydew is excreted after most of the protein is extracted from the phloem by the herbivore. Honeydew also normally contains trace quantities of amino acids not utilized by the herbivore (Way 1963). In Homoptera that are tended by ants, the herbivore is stimulated to excrete a droplet of honeydew from the anus when its abdominal posterior is antennated by the tending ant.

Honeydew is particularly prized by species of ants in the *Formica rufa* group (red wood ants of the Old World; thatching ants of the New World) (Weber 1935, Otto 1965, Cherix and Bourne 1980, Skinner 1980). The *F. rufa* group is composed of about 50 species worldwide, with a generally holarctic distribution. Colonies are among the largest in ants, and can consist of single-nest colonies of up to a million workers, or multi-nest supercolonies having worker populations in the tens or even hundreds of millions (Higashi and Yamauchi 1979, McIver et al. 1997). Species of *F. rufa* are typically ecologically dominant, suppressing populations of other arthropod species that occur nearby (Cherix and Bourne 1980). Workers within colonies vary in body length between 4 and 8 mm; the Old World common name (red wood ant) stems from the fact that the larger workers have a thorax that is generally reddish in color. The New World common name (thatching ant) describes the type of nest built by most *F. rufa* group species—large dome-shaped primary nests of woody material collected nearby (Fig. 1).

Honeydew is a valuable source of amino acids, carbohydrates, and water and, in most *F. rufa* group species, it comprises a critical portion of the colony's diet. It is used to nourish the brood and queen and as energy for the workers (Wellenstein 1952). In the Great Basin Desert, honeydew is included almost universally in the diet of thatching ants; of 213 colonies of various thatching ant species ex-

Fig. 1. Primary nest of *F. obscuripes* colony at Pike Creek, southeastern Oregon, July 1987. Nest diameter = 65 cm, nest height = 35 cm. Photograph by Trygve Steen.

amined in the current study, only 3 were not actively tending Homoptera for honeydew during the foraging season.

Because honeydew is so important to thatching ant colonies, understanding the foraging ecology of these species requires knowledge of how it is collected and transported to the primary nest, where the queen lives and where the brood and young workers are nourished. Of the 17 thatching ant (*Formica rufa* group) species known to occur in the Great Basin Desert (Wheeler and Wheeler 1986), the western thatching ant *Formica obscuripes* Forel is among the most common and widespread (Fig. 2). The purpose of this study was to describe the mechanics of honeydew harvest in the western thatching ant, with the assumption that foraging behavior in this species would reflect behavior for the species group as a whole.

Materials and Methods

The western thatching ant was studied between June 1986 and August 1991 at Pike Creek, 160 km southeast of Burns, OR (118°
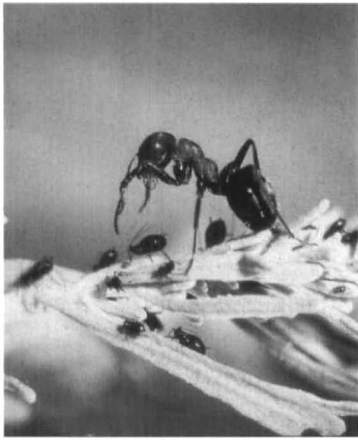
Fig. 2. Grooming *F. obscuripes* tender in company of aphids *(A. artemisicola)* on sagebrush at Pike Creek, southeastern Oregon, July 1987. Marked worker is 6.0 mm in length. Photograph by Trygve Steen.
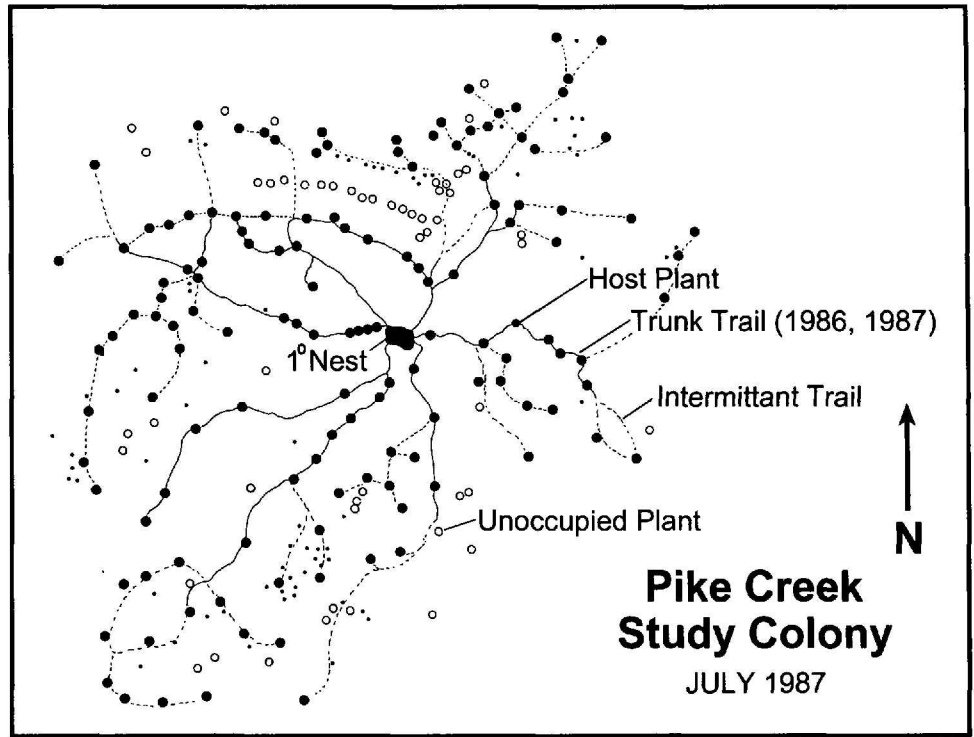

Fig. 3. Trail structure and host plants of Pike Creek study colony, 8–26 July 1987.

32' 30" W, 42° 32' 30" N). Pike Creek flows off the eastern scarp of Steens Mountain in the northern Great Basin, a high desert characterized by cold, dry winters and warm, dry summers (Franklin and Dyrness 1988). The study site was defined by a perimeter extending from 1,290 to 1,355 m elevation east to west (perpendicular to the mountain's scarp) and encompassing the northern half of the creek's alluvial fan from north to south. In total, 12 colonies were active within the 10-ha study site during the study period. Workers foraged for honeydew on several species of forbs and shrubs (Table 1) and scavenged for arthropods in the area surrounding each primary nest.

Eight colonies were observed at Pike Creek during 6 field seasons (1986–1991). This article describes work conducted on an average-sized colony (≈25,000 individuals) that had a large tending population (≈1,500 workers) during the summers of 1986 and 1987. This colony was selected for intensive study because the orientation of the primary nest and the distribution of trunk trails allowed easy observation without disturbing the trails or ants working on the nest surface. The patterns of honeydew harvest observed at this colony were similar to the other 7 colonies examined during the 6-yr study.

The colony was mapped in detail in July 1987, including the position of the primary nest, aphid-occupied host plants, trunk trails (semipermanent primary transportation arteries), and intermittent trails (trails on which workers traveled intermittently during times of peak use) (Fig. 3). Foraging activity was observed from June through August 1986 and 1987, with special note taken of the movement of workers with distended gasters. On 27 and 28 July 1986, the number of workers traveling in both directions past a wire

flag on the colony's primary trunk trail was correlated with trail temperature, taken at the flag in the shade within 1 cm of the ground surface. Trail temperatures also were taken throughout the summer of 1987 so that we could place trail traffic patterns in a seasonal context.

Research on the behavior of workers associated with host plants was based on intensive observation of individuals marked uniquely with small colored and numbered plastic disks (bee numbers, Charles Graf, Frankfurt, Germany) (Fig. 4). Aside from irritation shown by some workers immediately after marking, bee numbers had no discernable effect on behavior. Workers seen on or around host plants were marked and observed, including those that tended aphids and those that scavenged or patrolled at the plant base.

Fidelity to particular host plants and even to specific aphid groups is well known in the western thatching ant (Herbers 1977). To describe fidelity and tender replacement through time, workers on 23 sagebrush (*Artemesia tridentata* Nuttall) plants with easily observed canopies were followed daily between 25 May and 8 August 1987. Although virtually identical behavior (including fidelity) was observed in tenders working on every host plant we studied, for the sake of brevity we report results from 2 representative host plants, sagebrush plants 6E and 13S.

On plant 6E (6 m east of the primary nest), we marked all observed tenders (*n* = 15) between 16 and 30 July 1986. On each day in early August 1986, we displaced several individual tenders from their established positions on the plant to other positions on the same plant and to other plants within the colony's foraging territory,

Table 1. Homopteran species tended by the western thatching at Pike Creek and their host plants.

Host plant species	Homopteran species	Family
Artemisia tridentata Nuttall (sagebrush)	*Artemisaphis artemisicola* (Williams)	Aphididae
	Zyxaphis canae (Williams)	Aphididae
	Pulvinaria sp.	Coccidae
Chrysothamnus viscidiflorus (Hook) Nuttall (green rabbitbrush)	*Zyxaphis chrysothamni* (Wilson)	Aphididae
Tetradymia sp. (horsebrush)	*Aphis* sp.	Aphididae
Lupinus caudatus Kellogg (Kellogg's lupine)	*Aphis* sp.	Aphididae

and then we observed their subsequent response. We report the response of only 1 such worker in this article, tender 32°Y (#32, yellow with black dot), because it exhibited a behavioral response that was representative of every other tender similarly displaced.

To determine the mechanics of honeydew harvest over the daily cycle, workers were observed for a 24-h period (23–24 July 1987) on a 2nd host plant (plant 13S). Plant 13S was a small sagebrush plant (70 cm high) located 13 m south of the primary nest and was chosen because the entire canopy was readily visible by 2 observers at any given time. Between 1 and 22 July, all workers associated with plant 13S were marked with bee numbers. Beginning at 1200 hours on 23 July, we recorded the positions of all visible workers every 15 min, including those tending aphids in the canopy, those present on the plant trunk or in the secondary nest at the plant base (a shallow excavated hole at the ground surface surrounding the plant trunk as it entered the ground [McIver and Steen 1994]), and those on the ground within 0.5 m of the host plant. Observations at night were taken with headlamps fitted with red filters. We also recorded when workers left their host plant to return to the primary nest. During this 24-h period, we recorded the activities of 16 workers (9 tenders and 7 honeydew transporters); in this article, we report on 1 representative worker engaged in each task.

Because age-related behavioral change (temporal polyethism) is well known in *F. rufa* group species (Otto 1958), we wanted to describe the form and direction of this change in relation to tending in the western thatching ant. We studied temporal polyethism by marking callow adults (collected as they occasionally emerged at the primary nest surface in June 1987), primary nest maintenance workers, exuvia/refuse removers, tenders, transporters, and scavengers and, then, observing these workers for most of an entire foraging season (May–August 1987). We expected to find age-related changes in behavior in the direction of foraging, with callows and primary nest-associated workers eventually becoming foragers (scavenging and tending) as the season progressed.

To place honeydew harvest in a seasonal context, we followed the careers of individual tenders by marking the majority of tenders on 3 host plants from late May to mid-August 1987. We report the July schedule for plant 13S as a representative progression of tenders through time.

Results

During the summer of 1987, the Pike Creek study colony harvested aphid honeydew from 266 of 320 sagebrush and rabbitbrush (*Chrysothamnus viscidiflorus* [Hook]) plants that were growing within the foraging territory (83% use) (Fig. 3; plants were not counted in 1986). Within a 5-m radius of the nest, all available sagebrush and rabbitbrush plants were occupied continuously by aphids and their tenders. The host plants were accessed by a system of semipermanent trunk trails that originated at the primary nest and led to a system of intermittent trails accessing plants on the periphery of the colony territory.

During each day between mid-May and mid-August, the colony's trail system was used chiefly between 0600 and 0930 hours and between 1630 and 2030 hours (Fig. 5). Workers typically were absent from trails during the hottest part of the day (between 1030 and 1600 hours) and occurred on trails at a much reduced level at night (between 2100 and 0530 hours). This pattern was less distinctive on rainy or cloudy days. In particular, workers were rarely seen on trails when surface temperatures exceeded 40°C. Between 20 May and 8 August 1987, trail temperatures at noon exceeded 40°C on 55 of the 81 foraging days (68%).

Honeydew was transported back to the primary nest during the morning (between 0600 and 1000 hours) and late afternoon (be-

Fig. 4. Worker marked with bee number (white 85) and unmarked nestmate tending aphids on sagebrush, Pike Creek, southeastern Oregon, July 1987. Photograph by Trygve Steen.

tween 1700 and 2100 hours) by 2 types of workers: tenders and honeydew transporters (Fig. 6). Workers that tended aphids spent the majority of the day actively tending, interspersed with frequent visits to a secondary nest (worker retreat with no brood) at the plant base. Worker 84 exhibited behavior typical of individuals classified as tenders. Tenders appeared to transfer much of their collected honeydew during the day and night to larger workers that spent most of their time at the plant base. Worker 13 exhibited behavior typical of honeydew transporters, individuals who received honeydew from tenders at the plant base. Observations of transporters indicated that, in addition to receiving honeydew, these workers scavenged for arthropods in the vicinity of their host plant. Tenders and transporters hence worked together to deliver honeydew to the primary nest using a chain transport system. The chain transport hypothesis involving tenders and honeydew transporters is supported by observations that workers at the plant base rarely tended aphids yet often returned to the primary nest with distended gasters, and extended trophallaxis commonly was observed between tenders and larger base-associated workers at the entrance to the secondary nest.

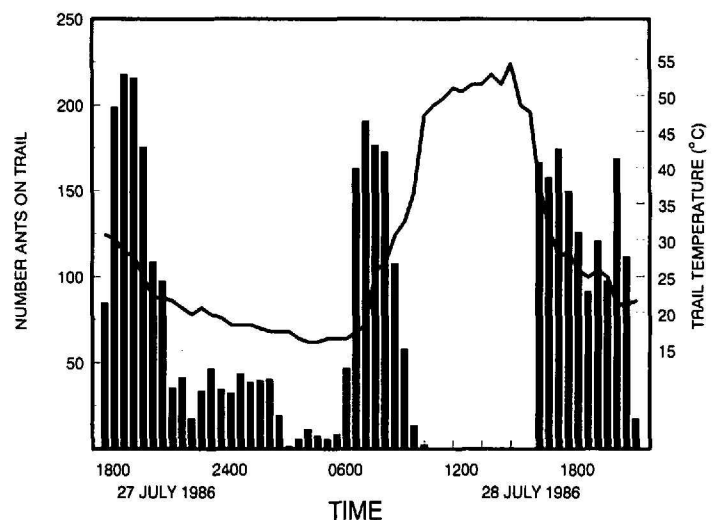The fidelity seen on plant 13S (Fig. 6) was typical of each tender

Fig. 5. Trail temperature and activity of workers on northeast trunk trail of Pike Creek study colony, 27–28 July 1986.
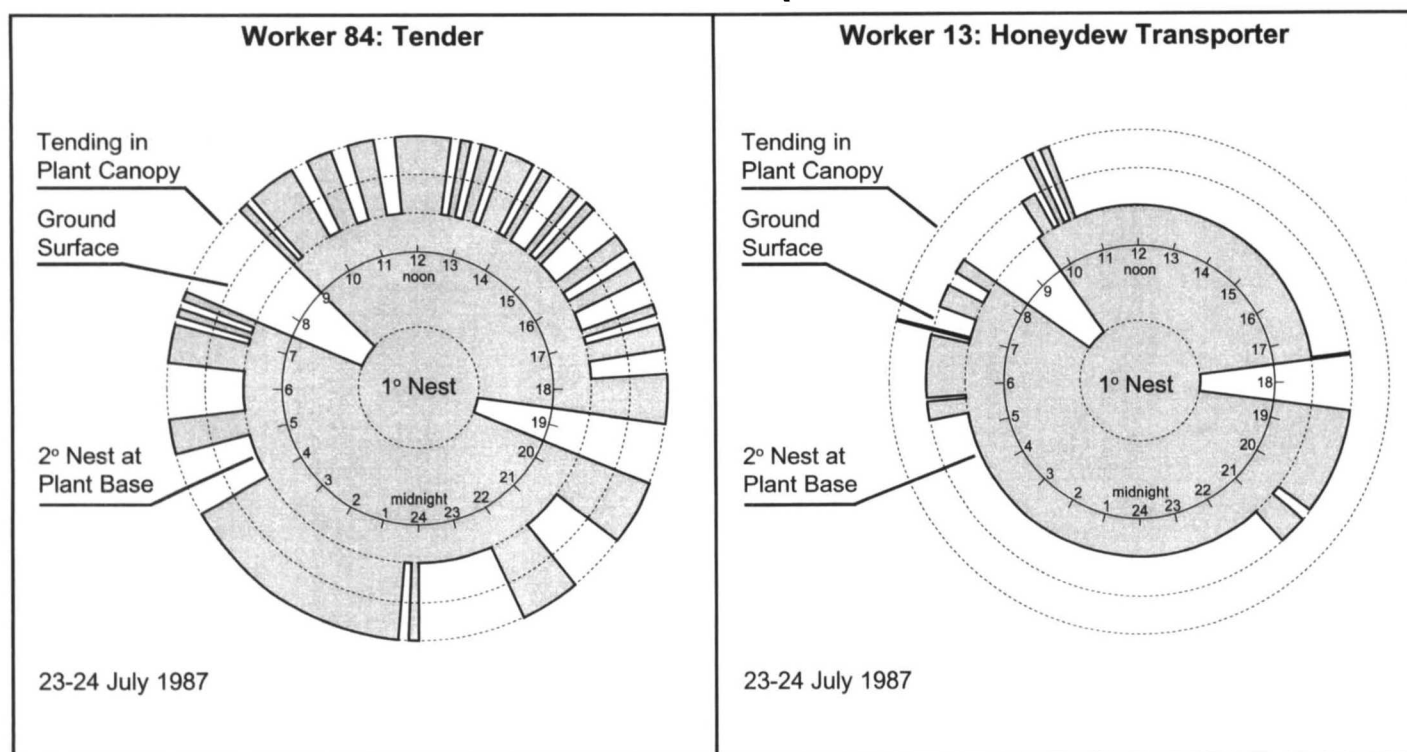
Chain Transport

Fig. 6. Activity over 24-h period of tender (worker 84) and honeydew transporter (worker 13) on plant 13S, Pike Creek study colony, 23–24 July 1987.

marked during the study. Although most tenders visited several distinct aphid populations on a given host plant during their tending lives, a majority of their visits were focused on 1 or 2 aphid groups. Fidelity to particular host plants or even to particular aphid groups could not be broken by displacing tenders to other localities. Tender 32°Y for example, initially marked on the north portion of a sagebrush plant 6 m east of the primary nest (plant 6E), was displaced

Table 2. Tending chronology of a typical worker (tender 32°Y) marked originally on north branch of plant 6E (6EN), Pike Creek study colony, 4–13 August 1986.

Date in Aug. 1986	Time, hours	Location	Task
4	0850	6EN	Tending
4	1945	6EN–6ES[a]	Tending
5	0714	6EN–6ES[a]	Tending
6	2010	6EN–6ES[a]	Tending
6	2322	6EN	Tending
8	0711	6EN	Tending
8	2006	6EN	Tending
8	2100	6EN	Tending
8	2145	6EN–6ES[a]	Tending
9	0615	6EN	Tending
9	0646	6EN	Tending
10	0640	6EN	Tending
11	2007	6EN	Tending
11	2130	6EN–6ES[a]	Tending
12	0911	6EN	Tending
12	0952	6EN–8W[a]	Tending
13	0804	6EN–8W[a]	Tending
13	0945	6EN–8W[a]	Tending
13	1944	6EN	Tending

[a] Indicates experimental displacement of tender to south branch of plant 6E (6ES) or to plant 8W (14 m west of 6E). Subsequent observation at location 6EN indicates return of the tender to her original location.

several times to the south portion of the same plant, yet always returned to her original tending locale (Table 2). Even displacement to an aphid-occupied plant 8 m west of the primary nest did not break her fidelity, for she returned to her original tending locale after the trunk trails opened during the following trail activity period. This behavior was typical of 14 other tenders similarly displaced on plant 6E; each returned to her original tending locale when displaced either to another locale on the same plant or to another host plant altogether.

Daily observations on plant 13S indicated that the individual composition of the tending population on 2 July 1987 was entirely replaced by 28 July, with some tenders seen on just a single day and others for as long as 26 d (Fig. 7). Of the 49 individuals whose entire lives as tenders occurred within the 29-day period, the average tending period lasted 7.96 d (SD = 8.09); 12 lasted a single day and 2 lasted 26 d. Although the previous duties of the tenders of plant 13S were not known, marking data suggest that most tenders were older individuals that had performed other primary nest-associated duties (e.g., nest maintenance, exuvia removal) prior to work as tenders. Of 29 workers whose adult lives were documented by >12 observations during >10 d, 8 individuals showed signs of age-related change in behavior. Six individuals changed from primary nest maintenance workers to scavengers and 2 changed from primary nest maintenance workers to tenders, including one individual that was marked initially as a callow. By comparison, none of the 2,056 workers initially marked as tenders was observed subsequently performing primary nest-associated duties.

Discussion

Western thatching ant colonies of the Great Basin Desert are highly organized in their collection and delivery of honeydew to the primary nest. During the middle of the day, workers tend aphids in the canopy of their host plants and are largely absent from the trails when temperatures on the ground exceed ≈40°C.
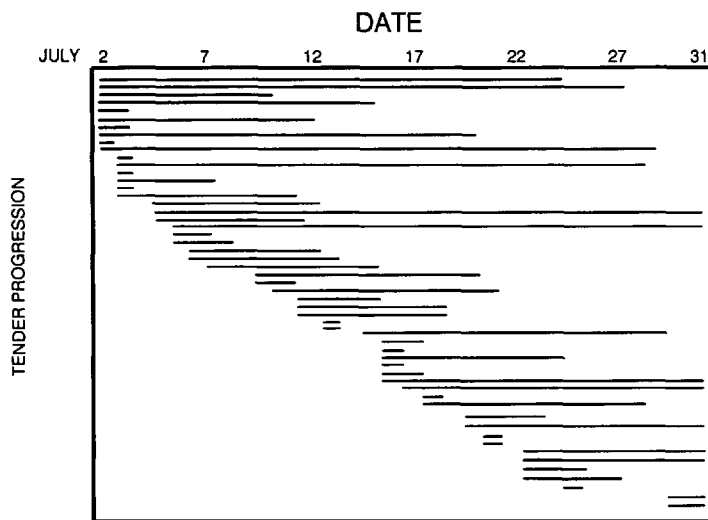
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Fig. 7. Tender visitation through time on plant 13S, Pike Creek study colony, 2–31 July 1987. Each row represents 1 tender.

During midday, each tender visits aphid aggregations in the plant canopy, interspersed with numerous trips to the secondary nest at the plant base. During each canopy trip, she typically collects honeydew from a number of aphids, and, during each trip to the plant base, she delivers this honeydew to much larger workers (transporters) for storage during the day. Each tender shows a unique pattern of tending activity, consistently visiting the same aphid aggregations during each trip to the plant canopy. The typical transporter remains in the secondary nest at the plant base or makes occasional forays out to scavenge within the shadow of her host plant.

As temperatures cool by late afternoon, tenders and honeydew transporters begin to stream back to the primary nest along well-defined trunk trails, their crops filled with honeydew. The midday pattern of isolated patches of worker activity breaks down and the colony is seen as a hub of central activity with dense spokes of fast-moving workers radiating into and out of it. Each tender or transporter makes at least one trip to the primary nest during the evening. As light fades, trail activity wanes, and the colony regains its midday structure by nightfall. Tending activity in the plant canopy continues at a reduced level throughout the night, with each worker once again making several trips back and forth between the canopy and the nest at the plant base. About 1 h before sunrise, workers begin to return to the primary nest once again, laden with honeydew collected during the night. Each worker makes at least 1 trip to the primary nest between daylight and when the ground surface heats to 40°C, 3–4 h later. By midmorning, the colony regains its midday form, and the cycle begins anew.

This general pattern is repeated each warm, summer day. However, under cool or cloudy conditions, differences between the morning/ evening and midday/nightime patterns of activity are reduced. Over the summer, tenders at each aphid aggregration are replaced constantly, with some working as much as 4 wk before disappearing altogether. Early in their lives, future tenders perform other social tasks, such as rearranging nest material or carrying out exuvia or refuse.

This highly organized harvesting system underscores the importance of honeydew in the life history of the western thatching ant. Honeydew has at least 2 principal functions in this ant species. First, it serves as food for workers, larvae, and the queen (Wellenstein 1952). Second, because the aphids that supply honeydew are widely distributed across the ants' foraging territory, the persistent harvest of honeydew places the workers in an ideal position to defend that territory and provides them with energy for the defense.

Taken together, the behavioral components of the harvesting system (temporal polyethism, foraging fidelity, chain transport, and the trunk trail system) provide the colony with a reliable means to collect and deliver honeydew to the primary nest and to maintain a steady supply of widely distributed workers for territorial defense. Yet, although the harvesting system as a whole appears to be highly organized, it is nonetheless built from behavioral components that are common in other ant species that vary considerably in their foraging habits and modes of territorial defense.

For example, temporal polyethism is nearly ubiquitous in ants and appears to be a fundamental feature of social insects in general, including termites, ants, bees, and wasps (Wilson 1971). As in every case studied, behavioral change with age in the western thatching ant is in the direction of foraging, with younger workers undertaking tasks within or close to the primary nest (Otto 1958).

Foraging fidelity is thought to be an adaptation for acquisition of persistent (Rosengren 1977, Traniello 1987) or aggregated resources (Schmidt-Hempel 1984) and may increase speed to and from the primary nest (Wehner 1987). Yet foraging fidelity is very common in ants and has been reported in both territorial and nonterritorial species representing several major subfamilies including the Ponerinae (Deneubourg et al. 1987), Myrmecinae (Hölldobler 1976), Dolichoderinae (McIver 1991), and Formicinae (Økland 1931, Dobrzanska 1966, Ebbers and Barrows 1980, Fowler and Roberts 1980, Tilles and Wood 1986, Wehner 1987, O'Neill and Kemp 1990). Extreme fidelity to particular homopteran aggregations has been described for workers of *Formica* spp. in the *sanguinea* and *fusca* groups (Ebbers and Barrows 1980) as well as several species in the *rufa* group (Herbers 1977, Rosengren and Fortelius 1986).

The observation of chain transport in the current study confirms earlier reports on the same species (King and Walters 1950, Siebert 1992). Chain transport in thatching ants not only increases honeydew flow to the primary nest, it links larger-bodied scavengers to the honeydew collection process and places them alongside the smaller tenders for potential territorial defense. It also has been reported as part of the recruitment process in the aggressive territorial ant *Oecophylla longinoda* (Latrielle) (Hölldobler and Wilson 1978). Yet chain transport of foraged material has been described in several nonterritorial species including the myrmicine *Daceton armigerum* (Latrielle) (Wilson 1962) of the Neotropics, the ponerine *Megaponera foetens* F. of Africa (Levieux 1966), and the formicine *Camponotus pennsylvanicus* (DeGeer) of North America (Pricer 1908, Fowler and Roberts 1980).

Trunk trails serve to distribute western thatching ant workers into the foraging territory quickly and, thus, are an important component of territorial defense. Many ant species use semipermanent trunk trails to access foraging localities, especially for the harvest of persistent resources like honeydew and seeds (Carroll and Janzen 1973). In many species of ants that use trunk trails, however, aggressive territorial defense either does not occur or occurs only adjacent to the trunk trails themselves (*Pogonomyrmex* spp.; Hölldobler 1976).

In summary, it is the integration of simple behavioral components that provides the western thatching ant colony with a well organized system for honeydew harvest. The tendency of workers to develop into foragers with age, to become faithful to particular aphid herds, to feed other hungry foragers, and to follow trunk trails are all simple behavioral feats that, when combined, result in a high degree of organization.

The description of foraging systems, and how they are integrated into life histories is a necessary step toward building a theory that explains the considerable variation in life history strategies employed by ants and other social insects (Tschinkel 1991, Bourke and Franks 1995). The highly organized system of honeydew har-

vest in the western thatching ant suggests that honeydew is at the center of this species' life history. Further research should aim to pinpoint the significance of honeydew during this ant's colony growth and annual cycle.

Acknowledgments

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