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Foraging and Leaf-Cutting of the Desert Gardening Ant *Acromyrmex versicolor versicolor* (Pergande) (Hymenoptera: Formicidae)

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Summary. Four colonies of the desert leaf-cutter ant *Acromyrmex versicolor versicolor* (Pergande) located 30 miles N.E. of Tempe, Arizona were observed over a 7 month period. The ants utilized trails in foraging, a characteristic of higher attines, as well as foraging singly, a typical pattern among the more primitive gardeners. The ants cut and collected both dry and green vegetation with dry grasses comprising the bulk of the forage. The ants increased their cutting of green vegetation after significant rainfall but collected dry grasses almost exclusively during dry periods. Detailed macro-motion picture analysis of leaf-cutting revealed that the desert gardener utilized a unique technique for cutting compound desert leaves.

Introduction

A number of reports have been concerned with foraging in the attine genera *Atta* and *Acromyrmex* (Lutz, 1929; Hodgson, 1955; Moser, 1967; Cherrett, 1968; Murray, 1972; Lewis *et al.*, 1974). These papers have focused on the environmental cues initiating foraging, the effects of weather on foraging, and trail flow patterns. In addition, they have discussed trail pheromones and other facets of general attine biology.

Despite considerable literature on the genera *Atta* and *Acromyrmex*, the behavior of *Acromyrmex versicolor* (Pergande) of the southwestern United States remains relatively unknown. With the exception of taxonomic reports, W.M. Wheeler (1907) was the first to record observations on the biology of *A.v.versicolor* and later (1917), he described its nuptial flight in Arizona. More recently an M. S. thesis (Murray, 1972) presents data on foraging in *A. v. versicolor*. Apparently the biology of the Texas subspecies, *A. v. chisosensis* (Wheeler), is unknown and therefore these three reports represent the total literature on *Acromyrmex versicolor*.

In contrast to other attines studied, *A. v. versicolor* exhibits several unique behaviors in its trail patterns, choice of forage, and mechanisms of leaf-cutting. To the best of my knowledge, the techniques of leaf-cutting have not been critically studied and this paper presents, for the first time, a detailed analysis of leaf-cutting.

Methods

Field observations were conducted from June 30, 1973, through February 10, 1974. I studied four colonies situated in a 20 m by 100 m study area located approximately

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30 miles N.E. of Tempe, Arizona, near the intersection of Bush Highway and the Sahuaro Lake turnoff. According to Weber (1972) each colony rigorously excludes noncolony members. By marking ants and introducing them into different nests, I determined that the four study nests were indeed distinct colonies. The colonies were at an approximate elevation of 600 m and situated in sandy soil on level ground that formed a small plain at the base of several large hills.

The vegetation in the study area consisted of creosote-bush (*Larrea tridentata* Coville), ironwood (*Olneya tesota* Gray), mormon tea (*Ephedra fasiculata* A. Nels.), mesquite (*Prosopis velutina* Woot), catclaw acacia (*Acacia greggi* Gray), heron-bill (*Erodium cicutarium* (L.) L'Her), turpentine broom (*Thamnosma montana* Torr. and Frem.), globemallow (*Sphaeralacea* Kearney), bur sage (*Franseria deltoidea* Torr.) and various grasses of the family Graminae.

Trail flow from the nest was recorded with a hand tally counter and consisted of a 60 sec count of all ants proceeding away from the nest. Trail flow to the nest was recorded as above except two separate 60 sec counts were taken; the first reflected the number of ants carrying vegetation to the nest and the second recorded ants returning to the nest "empty handed".

I recorded soil surface temperature on 27 different observation dates from August 9 through December 10, 1973. Temperatures were recorded with a YSI Model 46 tele-thermometer accurate to 0.15° C. The probe was covered with approximately $^1/_2$ cm of loose soil and placed in the full sun. I normally recorded temperatures at 15 min intervals.

Bolex 160 Macrozoom and Bolex Reflex (with +10 close-up lens) eight mm motion picture cameras were used to film leaf-cutting.

Results

I. Trails

From June 30 to November 14, 1973 (37 observation days), *A. v. versicolor* formed distinct files on physically distinguishable trails while foraging for vegetation. However, beginning November 19 after heavy rains the ants no longer formed distinct columns but were dispersed around the nest opening in an approximate two meter diameter circle while collecting vegetation from scattered grasses and herbs. Foraging columns were not observed after November 14, 1973.

Trails were cleared of all vegetation; portions of the trails that passed over areas devoid of vegetation (sandy washes) were visible only in the presence of ant activity. Trails were from 10 to 14 cm in width and extended up to 17 m from the nest. Three of the colonies used more than one path per nest although one of the trails of each nest carried the bulk of leaf-cutter traffic. Trails were distinct for most of their length but their terminals were highly diffuse; it was here that cutting and collecting took place. Ant files on trails leading to a bush became dispersed from one to one and one-half meters from its base.

Foraging maps of a single colony (July 5 through November 14, 18 maps) showed that the proximal portions of the colony's trails were utilized repeatedly over long periods of time (at least 4 months, Fig. 1). The ants changed the ultimate destination of the trail by altering the direction of its distal portion. Thus, the proximal segments of the trail were permanent while the distal parts changed directions to connect with various flora.

Fig. 2 shows that the rate of ant trail flow leaving the nest in a daily cycle remained relatively constant until surface temperatures reached 34°–38° C. Recordings on October 26 were from a different colony than October 10, 15, and 29 data in Figs. 2–4. Counts on October 26 were taken close to the nest (<1 m)

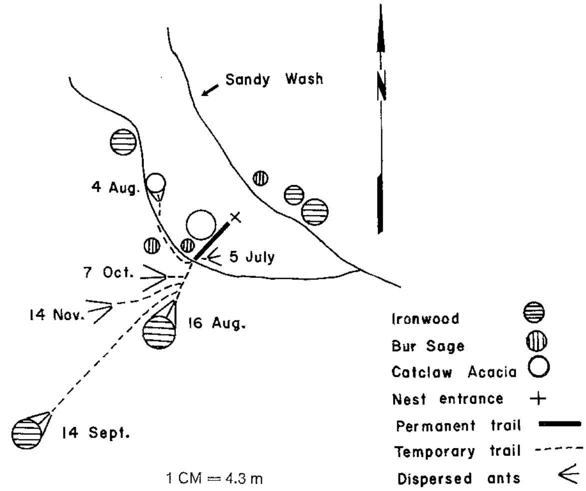

Fig. 1. Foraging map of one *A. v. versicolor* colony

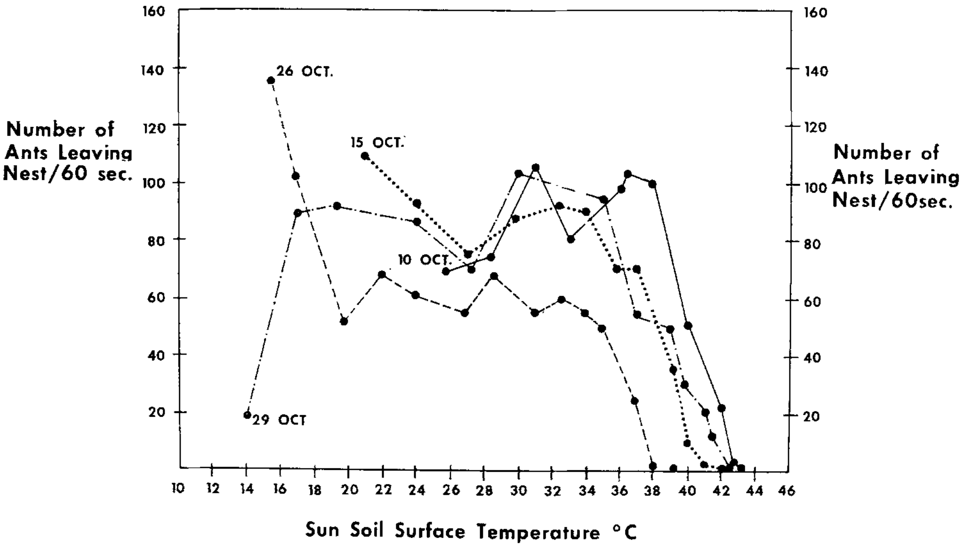

Fig. 2. Rate of ant trail flow from nest

and the beginning high number of ants leaving the nest reflects the initial surge of ants at the start of foraging. Counts on October 10, 15, and 29 were taken on the trail 2 m from the nest at which point the initial clump had dispersed into a rather stable trail flow.

In contrast to the relatively constant ant flow leaving the nest in Fig. 2, Fig. 3 shows a progressive rise in the number of ants returning to the nest during the foraging cycle. The number of returning ants increased until critical

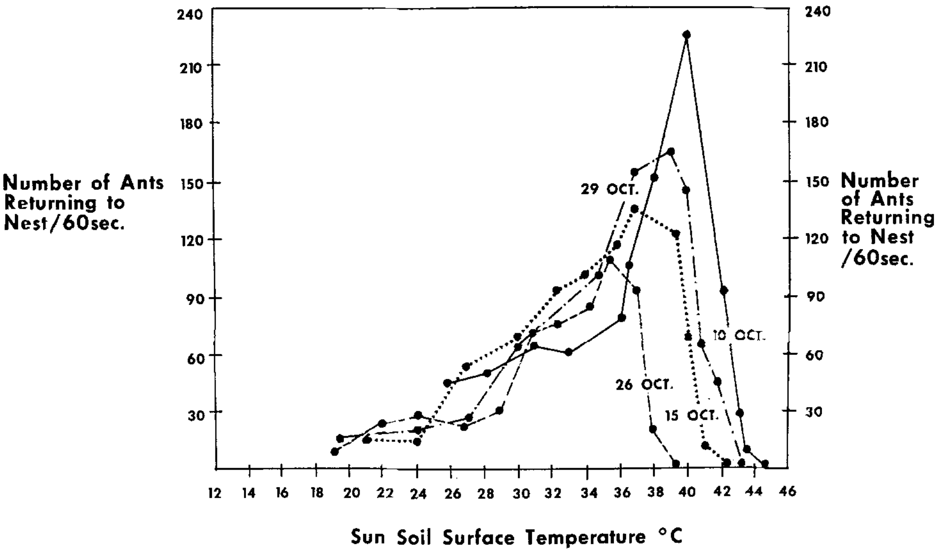

Fig. 3. Rate of ant trail flow toward nest

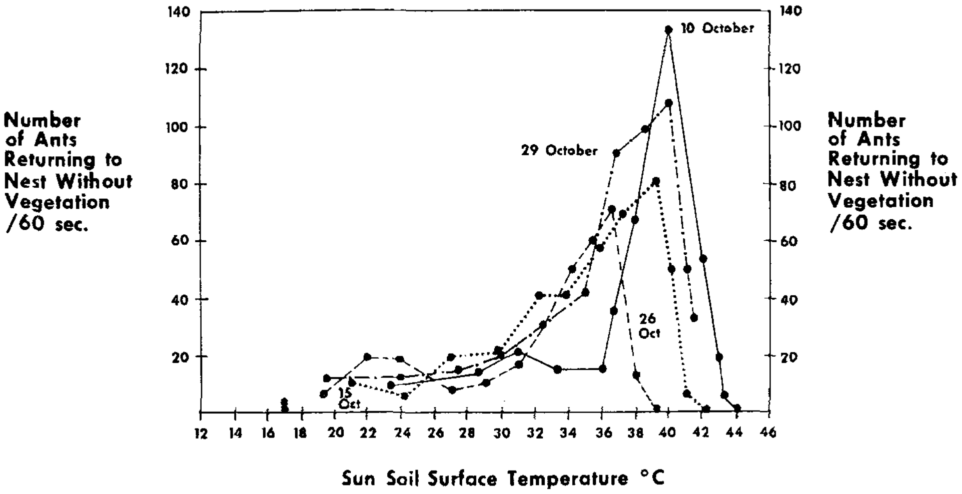

Fig. 4. Rate of unladen, return ant trail flow

maximum temperatures of 36°–40° C were reached. At this point the number returning dropped drastically and trail activity ended in a short time. In Fig. 4 the flow of ants returning to the nest without vegetation shows a sharp increase at about 30°–36° C. Apparently the ants, sensing the rising temperatures, returned to the nest even though they had not secured vegetation.

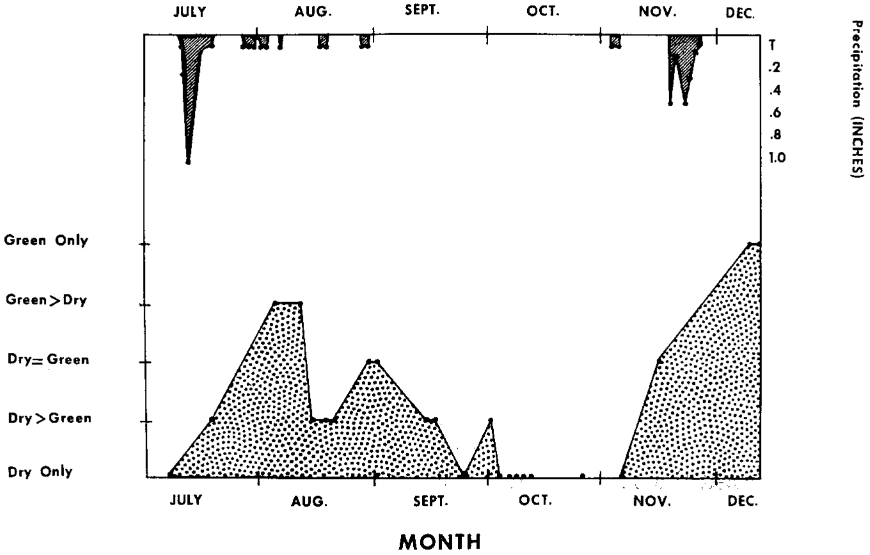

Fig. 5. Precipitation (Phoenix National Weather Service Monthly Summary) vs. relative amounts of dry and fresh green forage at one colony

II. Vegetation Collected

A. v. versicolor cut and collected desert ironwood, mesquite, catclaw acacia, and dry grasses between June 30 and November 14, 1973. Subsequent to November 14 forage consisted principally of heron-bill and some dry grass. The most commonly foraged vegetation throughout the study was dry grass. Data from foraging maps and field notes determined that the leaf-cutters frequently carried a combination of dry and green vegetation (20 of 31 observation dates) with dry plant material usually comprising the major portion of the forage. In most foraging cycles involving green leaf cutting, some dry vegetation (including previously cut and dropped leaves) was collected at the beginning of the cycle. Dry plant material was already being carried to the nest before the first ants had begun to cut fresh leaves. However, as the foraging column proceeded into the branches and ants began cutting, return plant flow gradually became totally green for those days that "green only" vegetation was graphed (Fig. 5).

The relative trail flow of dry, yellow vs. fresh, green vegetation was so obvious (either green or dry forage was highly preponderant) that sampling was not required to determine dry/green categories (Fig. 5). However, on three dates (August 31, September 1, November 12) heavy flows of both fresh green and dry vegetation were evident throughout the daily cycle. On these 3 days green forage was roughly categorized as equaling dry forage (Fig. 5).

The relative proportion of green vegetation gathered increased at the one monitored colony after significant amounts of rainfall. Rainfall during the study was minimal with only two periods, July 11–15 and November 19–25, showing significant precipitation. During extended dry periods ants almost exclusively cut and collected dry vegetation.

III. Leaf-Cutting

A. v. versicolor cut both dry and green vegetation. Sixty observations were recorded of individual ants cutting fresh vegetation but only 3 records of ants cutting dry vegetation were noted. I rarely was able to see ants cutting dry vegetation because of the dense over-cover of dry grasses even though loud cutting noises often accompanied ants foraging in the dry grass. Some of the dry, annual grasses in the study area were trampled and broken into short lengths by grazing cattle.

Green plants selected for cutting possessed small, portable leaflets or leaves. These plants included the desert ironwood, mesquite, catclaw acacia, and the heron-bill. Mormon tea had long, green, spear-like branches which were occasionally frayed but not cut by *A. v. versicolor.* In both the ironwood and heron-bill the ants secured entire leaves or several leaflets by cutting the petiole or rachis. In mesquite and catclaw acacia, the ants cut single leaflets at the petiolule.

The ants used the same cutting method on both leaves and leaflets. In the following account of cutting on mesquite, ironwood, and catclaw acacia, the term leaf refers either to a leaflet or leaf. Macro-motion pictures disclosed the following sequential components of leaf cutting: (1) the gardening ant walked along branches and over leaves for a considerable period of time, "pinching" leaves with its mandibles prior to the selection of one for cutting (the pinched leaves possessed distinct marks from the mandibles), (2) the ant walked up and down a leaf antennating it continuously prior to cutting, (3) the ant selected the narrowest portion of the leaf, usually the petiolule of leaflets, and clamped its serrated mandibles about it, (4) the ant moved its entire body alternately from side to side sometimes entirely girdling the petiole, petiolule or rachis. During cutting, the leaf was continually bent up and down at the cut as the ant extended and retracted its legs. The leaf-cutters used an entirely different cutting technique on the low, herbaceous heron-bill. The ants simultaneously pinched and pulled the petiole of the leaf thereby severing the entire leaf with one quick motion.

In the most common situation (30 of 60 observations) the ant cut the leaf, shifted it to a carrying position over the head, and carried it down the branch and trunk to the trail. Frequently (16 of 60 observations) the ant cut the leaf which then fell to the ground. These cut leaves littered the ground at the base of the bush or tree and were collected by foraging colony members on the following day prior to any resumption of cutting. After dropping a cut leaf, the ant resumed its search for a new leaf to cut. Dropped leaves were commonly lost while the ant attempted to shift them to a carrying position. The shift was accomplished utilizing the antennae and first pair of legs. The ant bent its head down and back to grasp the leaf so that when it raised its head the leaf was held in the mandibles above the head angled posteriorly. In the third situation (14 of 60 observations) both the ant and leaf dropped to the ground as it cut the leaf upon which it was supported. The ant fell clutching the leaf in its mandibles. Impact with the ground and underlying branches often jarred the leaf from the ant's grasp. The ant searched for the leaf, which, if located, was picked up and carried on the trail back to the nest. Fallen ants on the ground failing to find dropped leaves proceeded without vegetation back to the nest while ants losing their vegetation but landing in lower branches proceeded to search for other leaves to cut.

Artificial placement of *A. v. versicolor* workers and females on the author's arm revealed that leaf-cutters attempting to cut the skin were capable of moving each serrated mandible independently of the other in an alternating in and out fashion. Although this cutting technique was not observed in natural, leaf-cutting situations, its potential use may enable *A. v. versicolor* to cut small pieces from large leaves or flowers like its tropical attine counterparts.

Discussion

A. v. versicolor utilized distinct foraging paths during most of the study but in mid-November when scattered annual herbs became abundant, the ants began foraging singly. The use of trails is a conspicuous feature of *Atta* and *Acromyrmex* while primitive genera show intermediate stages leading to the formation of physically distinct trails (Weber, 1972). Apparently, *A. v. versicolor* retains the flexibility to use either foraging strategy. It is probable that when food resources are somewhat clumped (trees, bushes), the ants use distinct trails in gathering plant material, but when plants are more evenly dispersed, they forage singly.

It has been reported that *Acromyrmex versicolor* collects pieces of leaves from bushes and herbs rather than from grasses (Weber, 1972). This study does not support that statement since *A. v. versicolor* relied heavily on dry grasses as plant substrate for its gardens. Another contention, that *Atta* and *Acromyrmex* rely exclusively on pieces of fresh leaves and flowers to nourish their fungus gardens (Wilson, 1971) must also be amended.

The ants collected larger proportions of green vegetation after significant periods of rainfall. Murray (1972), working with the same species in Pima County, Arizona, found that foraging period length, number of colonies foraging, and number of workers foraging were greatest after a rainfall of more than 0.25 inches. It is thus highly probable that *A. v. versicolor* accelerates its fresh, green cutting after rains when tender, young growth is most prevalent. This appears to be the case for related species since Barrer and Cherrett (1972) determined that *Atta cephalotes* selected the young leaves on a plant for cutting. Cherrett (1972) found that the young leaves cut by *A. cephalotes* were thinner, more tender, more sappy, and less dense than randomly collected samples.

According to Weber (1972), *Atta and Acromyrmex* cut an arc from a leaf; *A. v. versicolor*, surrounded by desert plants with compound leaves, severs the narrow petiole, petiolule, or rachis of a leaf or leaflet thereby leaving the collected vegetation relatively intact. The small leaflets and leaves are "pre-cut" in the sense that they are the ideal size for carrying.

The mechanisms of attine leaf-cutting as described by Weber (1972), do not represent the technique employed by *A. v. versicolor* in desert environments. According to Weber (1972), "the mandibles are applied to opposite sides and they start a cutting action, alternately closing one mandible and the other". *A. v. versicolor* clamps its serrated mandibles around a stem-like appendage and moves its entire body from one side to the other often entirely girdling the petiole, petiolule, or rachis. The ant does not move its mandibles independently although it is capable of such movement. This mode of cutting is evidently adaptive for cutting stem-like plant parts. Cutting methods of other attines are probably more suited to cutting circular pieces from large leaves as found in tropical forests.

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