

FORAGING ACTIVITY OF THE MEXICAN LEAFCUTTING ANT  
*ATTA MEXICANA* (F. SMITH), IN A SONORAN  
DESERT HABITAT (HYMENOPTERA, FORMICIDAE)

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SUMMARY

The largest ant colonies in the North American desert are produced by the Mexican leafcutting ant, *Atta mexicana* (F. Smith), in northern Sonora. The foraging behavior of *A. mexicana* is described for the first time. The ants use a system of tunnels and trails extending outward from the nest to reach target vegetation. Over the combined study periods from 1974 to 1977, one colony collected material from a total surface area of about 8,000 m<sup>2</sup>. The ants selectively attacked two species of winter annual plants and repeatedly utilized four perennials, two *Cercidium* spp., *Sapium biloculare* (S. Wats.), and *Larrea tridentata* Coville when the annuals were absent. In addition to fresh vegetation, they also collected dry material. The leafcutting behavior of the ants is variable, depending on the size and form of the plant material utilized. The ants foraged during the daytime in winter and spring but became largely nocturnal in summer.

ZUSAMMENFASSUNG

**Futtersammelaktivität der Mexikanischen Blattschneiderameise  
*Atta mexicana* (F. Smith) in der Sonora Wüste**

Die grössten Ameisenkolonien in der nordamerikanischen Sonora Wüste bildet die mexikanische Blattschneiderameise *Atta mexicana*, deren Futtersammelaktivitäten erstmalig beschrieben werden. Zum Futtersammeln benutzen diese Ameisen ein System aus Tunneln und Strassen, das vom Nest zu der Vegetation führt. Die Hauptbeobachtungskolonie wurde während mehrerer Jahre in den Monaten Dezember, Januar, März und Juli/August insgesamt 24 Tage lang kontrolliert. Sie sammelte während dieser Zeit Pflanzenmaterial auf einer Grundfläche von etwa 8000 m<sup>2</sup>. Die Ameisen schnitten bevorzugt zwei annuelle Pflanzenarten, nahmen aber, wenn diese fehlten, auch mehrere Arten von perennierenden Pflanzen an. Zusätzlich zu frischen wurden auch trockene Pflanzenteile eingetragen. Das Schneideverhalten der Ameisen war variabel und hing von Grösse und Form der Pflanzen ab. Die Ameisen sammelten in Winter und Frühling tagsüber und gingen im Sommer weitgehend zu nächtlicher Sammelaktivität über.

## INTRODUCTION

Fungus culturing ants of the genus *Atta* are conspicuous insects in most neotropical ecosystems and are serious pests in many areas (WEBER, 1972). The ants collect large amounts of living vegetation as substrate for the fungus upon which they feed. The genus is widely distributed in tropical forest and savanna areas in South and Central America. Two species, *Atta texana* (BUCKLEY) and *Atta mexicana* (F. SMITH), have ranges extending northward to the southern border of the United States. *A. texana* occurs along the Gulf of Mexico in Tamaulipas, Mexico, and in eastern Texas and Louisiana (MOSER, 1967). *A. mexicana* ranges from Guerrero, Mexico to Arizona in the north (BYARS, 1949). *A. mexicana* spans a range of habitats from Veracruz rain forest to the Sonoran Desert, at elevations from sea level to over 2000 meters (SMITH, 1963).

Despite its unique distribution over a wide variety of environments, detailed literature on the field behavior of *A. mexicana* is absent. Comparative studies on foraging behavior of the Mexican leaf-cutter in a variety of habitats with differing vegetation type may be valuable from an ecological and economic perspective. This paper provides initial data on desert foraging behavior of *A. mexicana*. The temperature range of foraging activity, selection of substrate vegetation and leaf cutting behavior were studied in winter, spring and summer.

## PROCEDURE

Observations were conducted on colonies located along Mexico highway route two in northern Sonora. One colony (A) located 46 km. south of Sonoita, Sonora was the primary focus of study. This colony was examined in late December 1974-1976, in March 1975 and 1977, and on July 31 - August 1, 1975 (a total of 24 days). Seven other colonies were also located 24-46 km. south of Sonoita; one of these was nearly one km. from the roadside. The elevation in the study area ranged from approximately 400 to 500 m. The mean annual rainfall in the area is approximately 250 mm., based on records at the Organ Pipe Cactus National Monument visitor center, 10 km. north of Sonoita (1). Some prominent perennial plants in this study area included creosote bush (*Larrea tridentata* Coville), palo verde (*Cercidium floridum* Benth. and *C. microphyllum* (Torr.)), ironwood (*Olneya tesota* Gray), mesquite (*Prosopis velutina* Woot.), *Encelia farinosa* A. Gray, *Condalia globosa* Johnst., cholla (*Opuntia* spp.), senita (*Lophocereus schottii* (Engelm.) and sahuaro cactus (*Carnegiea gigantea* (Engelm.)). The large perennial *Sapium biloculare*

(1) National Weather Service records at the visitor center (elevation 400 m) for 1949-1973 inclusive.

(*S. Wats.*) was abundant in the vicinity of the northernmost colonies. We found 16 other ant species within the foraging area of colony A.

Ants carrying forage items were field collected and later measured with a calibrated ocular reticule under a dissecting microscope. During field counting, ants were arbitrarily classified as large, medium or small. Specimens of plant species attacked by the ants were collected for subsequent identification. In 1976 and 1977, ant trail routes were measured, and the linear distance from tunnel openings to the central nest was also determined for two colonies. The distances from these two colonies to individual plants of preferred perennial species was also measured. Air temperatures were recorded and soil exposure to sunlight was noted during foraging activity.

## RESULTS

### 1. Spatial distribution of nests and foraging activity

The central nest area of the *A. mexicana* colonies contained extensive accumulations of excavated soil in the form of craters, and large surface refuse piles of exhausted fungal substrate. The primary colony studied was located on the side of a small desert wash, and most other colonies were also situated near or on the margins of arroyos, on otherwise level ground. Foraging trails issued from a system of subsurface tunnels extending outwards from the central nests. The tunnels had surface openings 10-60 m. from the central nest area (fig. 1), and one appeared to extend under the paved highway from the nest of colony A. Tunnels were stable components in the foraging system; many tunnel openings used in December 1975 were still in use 15 months later. The ants foraged along the wash and highway, as well as in the open desert. Colony A foraged over a combined surface area of about 8000 m<sup>2</sup> during the study periods in 1975, producing several trails simultaneously (2). At the height of activity in March 1975, this colony produced 23 basal foraging trails, some of which produced auxiliary branches. The other colonies observed foraged in a similar manner over large surface areas. In general, the ants adhered to fixed, well worn paths during each study period, although a few trails were more transient and disappeared or shifted position. Short surface trails (about 10 m. in length) were common; the longest trail observed extended 70 m. At the terminus of the trails, the ants dispersed and foraged individually, or climbed into vegetation. The great majority of ants on the trails were media workers, but some submajors and a few majors were also observed (Table I).

(2) Colony foraging area was determined using a minimum convex polygon with vertices taken as the distal terminations of foraging trails.

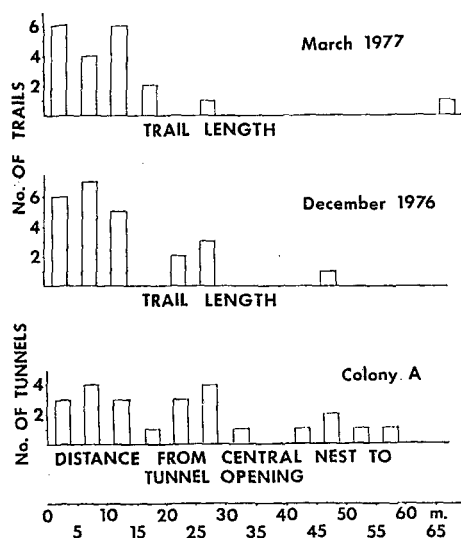


Fig. 1. — Minimum tunnel lengths and surface trail lengths for colony A.

Abb. 1. — Die kleinstmögliche Länge der Tunneln und Strassen von Kolonie A.

Table I. — Ants counted in a trail (30 December 1974). The workers of *A. mexicana* are highly polymorphic, with body length ranging from 2 mm. (minors) to 12 mm. (majors or soldiers).

Tabelle I. — Zahl von der Ameisen auf einer Sammelaktivitäts-Strasse (30 Dezember 1974).

	Minors	Medias	Submajors	Majors
Ants returning during a five minute period	0	22	1	0
Ants returning with forage items (5 min)	0	37	1	1
Ants returning with forage items (10 min)				
— large items	0	11	1	0
— medium items	0	26	1	0
— small items	0	17	0	0

2. Time, temperature, and foraging activity

In December 1974 and 1975 colony A foraged during the daylight hours. The daily maximum air temperatures ranged from 15 to 21°C. Foraging began when the air temperature exceeded 12°C in the morning (0900-1100 hrs.)

and activity was first noted on trails exposed to the morning sun. Foraging continued into the afternoon until the temperature dropped to 14°C, when leaf-cutting stopped and the workers returned to the tunnels before the air temperatures dropped below 11°C (1500-1800 hrs.). Ants remaining on the shaded surface exposed to an air temperature of 9.5°C were immobilized. Overnight freezing temperatures in winter will kill ants exposed on the surface (Mintzer, unpublished observation), but *A. mexicana* can forage during the afternoon on most winter days. The ants were actively collecting leaves at 14°C on an overcast day in late December 1975. In late December 1976, light rainfall did not interrupt foraging in progress.

In late March 1975, colony A was active during the day. On two days of clear skies, activity slackened on most trails in the early afternoon. Traffic ceased between 1400 and 1515 hrs. on the most insolated trails, as the ants returned to the nest during the warmest part of the day (about 26°C air temperature). On March 28, the sun was obscured during the early afternoon and foraging continued without interruption until observation ended at sunset. On six clear days in late March 1977, daytime maximum air temperatures ranged from 27-29°C. Colony A foraged in the morning and late afternoon. Traffic was interrupted between 1100 and 1600 hrs. on trails exposed to the sun, but continued through the midday hours on shaded trails. On two overcast days (March 25-26) foraging continued during the midday hours until interrupted by brief heavy rainshowers.

The ants foraged during the evening on July 31, 1975, when the daytime maximum temperature was 39°C at the Organ Pipe Cactus National Monument visitor center (56 km. north of colony A), a very typical value for July and August (3). The colony produced two large trails after sunset (2007 hrs.) as the air temperature dropped below 32°C. At 0730 on August 1, the ants were still active at a reduced level on the two trails. By 0816, the air temperature was 29°C and the few remaining ants were all returning to the tunnels. The trails were vacant by 0835 as the temperature reached 32°C.

### 3. Selection of vegetation as substrate

*Perennial plants.* Foraging trails extended to the base and up the trunk of target perennial plants. The ants climbed the branches into the crown; at any one time nearly all of the cutting ants were concentrated in one or two small areas in the leaf zone. The relative abundance of utilized perennial species varied greatly from one colony to another (Table II). The *A. mexicana* colonies cut material most frequently from creosote bush, *Larrea tridentata*. With two exceptions, all colonies were utilizing this resource during every observation period in December and March. The ants cut and collected the

(3) National Weather Service records at the visitor center (elevation 400 m) for 1949-1973 inclusive.

Table II. — Counts of utilized perennial plant species within 50 m. of two *A. mexicana* colonies in northern Sonora. Plants measured > 70 cm. tall (7854 m<sup>2</sup> area).

Tabelle II. — Zahl der benutzenden perennierenden Pflanzenarten (höhe > 70 cm) bis auf 50 m. von zwei Kolonien.

Colony	<i>Larrea tridentata</i>	<i>Olneya tesota</i>	<i>Cercidium floridum</i>	<i>C. microphyllum</i>	<i>Sapium biloculare</i>
A	216	4	6	8	1
D	21	8	0	25	31

inflorescences available on *Larrea* in addition to leaves in March 1977. Trails and tunnel openings were frequently littered with cut items from creosote bush. In December 1975, the two species of palo verde, *Cercidium microphyllum* and *C. floridum*, had leaves and were attacked by colony A and other colonies in the local area. In December 1976 and January 1977, colonies near palo verdes (*C. microphyllum*) with leaves were utilizing this resource. The ants also cut leaves from ironwood (*Olneya tesota*) during observation periods in December 1975, 1976 and in January and March 1977, although this plant was the least common large perennial around the *Atta* colonies. In January 1977, colony D (24 km. south of Sonoita) was cutting material from *Sapium biloculare*, which was locally abundant around this colony. Other colonies in the vicinity were also utilizing this plant. In March 1977 colony D ignored *Sapium biloculare* and collected *Larrea* leaves and dry vegetation instead. Mesquite (*Prosopis* sp.) and desert mistletoe (*Phoradendron* sp.) were attacked less frequently. The most abundant perennial in the vicinity of all colonies was *Franseria dumosa*. This small plant (usually under 50 cm. in height) occurred at an estimated average density of three individuals/m<sup>2</sup>, and was never attacked by *Atta*. Another common perennial, *Encelia farinosa*, was also avoided during all observation periods. Other perennial plants avoided were *Condalia globosa* and *Ambrosia ambrosioides* Cav.

*Annual plants.* In late March 1975 colony A was utilizing two species of annuals, *Plantago insularis* Eastwood, and a mallow *Sphaeralcea ambigua* Gray. *P. insularis* was an abundant small plant (usually under 10 cm. in height) which the ants attacked individually. *S. ambigua*, a larger plant (up to 50 cm. in height) was selectively attacked by the leafcutters, which left nearby conspecifics untouched. Few of the workers climbed more than 20 cm. in the vegetation, and flowering parts, stem sections and leaves were cut and collected by the ants. Media, submajor, and major workers were observed cutting vegetation. Major workers, the largest foragers, did not collect items of correspondingly large size, but often carried thick items such as inflorescences of *Plantago*. The ants appeared to ignore the perennial plants in the vicinity at this time. In 1975, no substantial winter precipitation was recorded until late December. The preferred annual species were represented

by small and widely scattered specimens, and the ants did not utilize them. In December 1976 and March 1977, annuals were utilized in addition to perennial plants, and inflorescences of *Plantago insularis* comprised a major fraction of forage items collected by colony A in March.

*Dry dead vegetation.* Dry vegetation was usually collected on the ground surface by individual foragers, although pieces were occasionally cut from dead standing vegetation. Foraging trails utilizing dry vegetation typically had a diffuse terminus, as the ants scattered and foraged individually. Colony A collected dry vegetation during periods in December 1975 and 1976, March 1977 and on July 31 - August 1, 1975. Colony D collected dry vegetation during January and March 1977. Dry leaves dropped by preferred perennial plant species comprised a major fraction of material collected. In December 1976 several trails from colony A collected dry leaflets of *Larrea tridentata* on the ground surface. In March 1977, two trails from colony D were collecting dry leaflets dropped beneath *Cercidium microphyllum*.

*Leafcutting activity.* *Atta mexicana* shows great variation in leafcutting behavior on different types of vegetation. In nearly all cases, the leafcutters stand on the piece they are attempting to slice off. The ants cut large semi-circular leaf segments from large-leaved plants such as citrus, mango, and oleander in cultivation at Alamos in southern Sonora. On narrow bladed annuals such as *Plantago insularis*, the cutting workers are nearly always oriented proximally, towards the base of the leaf, stem, or plant. The ants usually step over onto the remaining leaf surface as they complete cutting and pull the cut section free. The ants rarely cut pieces of a size smaller than they can stand on, and the pieces are often much larger than the foraging workers.

A different cutting behavior is observed on microphyllous desert perennials such as creosote bush and palo verde, which is similar to that described by Gamboa (1975) in *Acromyrmex versicolor* in Arizona. Most of these large desert perennials have small compound leaves connected to the stem by a petiole or rachis. The ants climb onto the small leaves and cut them at this convenient narrow junction. *A. mexicana* workers on palo verde can sever the rachis in about one minute, and often carry back an intact compound leaf cut through the petiole. The cutting ants tend to face towards the stem node, and stand at least partially astride the leaf. Of 151 cutting ants observed on four species of perennials and annuals, only 14 were oriented distally, towards the apex of the leaves or stem.

## DISCUSSION

In terms of biomass per individual colony and numerical size, *A. mexicana* probably exceeds all other desert inhabiting ant species in North America.

The Mexican leafcutting ant does not require a highly productive mesic ecosystem such as tropical rain forest in order to produce large colonies which are characteristic of the genus *Atta*. Although the colonies and their foraging areas are very large and conspicuous in the study areas, the colonies are widely scattered (foraging areas of different colonies are usually not contiguous), and the ant is uncommon or absent in many parts of Sonora.

The deep nests are well adapted to moderating desert extremes of temperature and moisture. The periods of foraging are largely determined by trail solar exposure and ambient temperature. The ants forage during the daytime in the winter months, and are active at night in summer, and their surface activity periods and temperature thresholds are similar to those of *Acromyrmex versicolor* (GAMBOA, 1976). *Atta* uses trail pheromones to organize foraging, allowing it to continue or initiate this activity in darkness (MOSER, 1967). Temperature extremes probably preclude continuous surface activity on a 24 hour schedule during most of the year; at Organ Pipe Cactus National Monument, average minimum air temperatures are 11°C or below during six months (November-April) and average daily maxima exceed 30°C during six months (May-October) (1). *Atta mexicana* is less tolerant of high surface temperatures in spring and summer than sympatric *Pogonomyrmex* species in Sonora. The use of long tunnels as a major component of foraging activity is characteristic of *A. mexicana*. The tunnels extend down at least 30 cm. before turning laterally, approximately parallel to the ground surface. These extensive tunnel systems reduce the exposure of the foraging ants to desiccation and temperature extremes at the air-soil interface, and place them effectively closer to the target vegetation which they must harvest during limited periods of surface activity each day. The initial construction of the tunnels probably requires a considerable energy investment by the ant colony, but the long term returns from harvesting additional resources over an enlarged surface area may be large. In southern Sonora and Tamaulipas, Mexico, *A. mexicana* colonies in scrub pasture and rangeland also produce foraging tunnels. It is interesting to note that foraging tunnels are encountered in *A. texana* in eastern Texas and Louisiana (MINTZER, unpub. observations; MOSER, 1967), but are poorly developed or nonexistent in the Costa Rican forest species *A. cephalotes* (L.) and *A. colombica* Guer. (L. ROCKWOOD, pers. comm.). Foraging tunnels appear to be a response to daily temperature extremes in the temperate zone and poorly shaded environments in Mexico.

When the preferred winter annual species were abundant, the colonies in northern Sonora did not utilize the perennial species. These ephemeral plants are a preferred winter food resource for *A. mexicana* in the Sonoran Desert. Desert winter annuals usually germinate after rains in December or January, mature slowly, and flower from March until May (SHREVE and



WIGGINS, 1964). The perennials are attacked before the annuals appear in winter. In the tropics, *A. cephalotes* also prefers soft, younger foliage (CHERRETT, 1973). A second group of annual species germinates after rains in July, August, and September, but the colony observed briefly in summer was not preferentially utilizing this resource. More observations on forager selection of midsummer desert vegetation are needed. Very few herbivores feed on creosote bush, and *A. mexicana* and its fungal partner appear to be utilizing a resource exploited by few other desert insects. Recent advances in biochemical technique (BOYD and MARTIN, 1975) may allow investigation of relationships between plant secondary compounds and choice of vegetation as substrate by the ants. Although the ants utilize some plants which are inedible or toxic to vertebrates (e.g. *Nerium oleander* L.), they are selective and completely ignore some common plants around their nests; presumably they are avoiding vegetation containing substances toxic to fungal enzymes and metabolism.

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