Leaf-cutting ant nests in temperate environments: mounds, mound damages and nest mortality rate in *Acromyrmex lobicornis*

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Abstract

The mounds of ant nests have been characterized as structures that facilitate the colonization of habitats subject to extreme temperatures. My objective was to investigate the importance of the mound of *Acromyrmex lobicornis* (Formicidae, Attini) in this process. In the most climatically rigorous environment that this ant genus lives (northwestern Patagonia), I determined (1) the temperature range within *Acromyrmex lobicornis* nest-mounds, (2) the influence of mound damages on the mortality or abandonment rate of *Acromyrmex lobicornis* nests, and (3) compared, from the existing literature, the distribution limits between the species of *Acromyrmex* that do and do not construct mounds. The mounds of *A. lobicornis* function as 'thermal buffers' by diminishing the effects of external thermal variations, and previous mound damage increased mortality or abandonment only of colonies with nest mounds constructed on bare ground. Mounds constructed on tussock plants increased their diameter faster and recovered better from perturbations. This may be due to the structural support of plant stems facilitating repair. At a larger scale, the species of *Acromyrmex* with mounds have more southerly range limits than species that do not construct mounds, indicating an important function of this nest structure for the colonization of temperate environments.

Keywords: *Acromyrmex*, disturbances, nest-architecture, nest microclimate, mounds, mortality, Patagonia.

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INTRODUCTION

The study of adaptations to climatically rigorous environments allows us to understand the mechanisms by which species can extend and keep their geographic range. In leaf-cutting ants, the decrease in species number of *Atta* and *Acromyrmex* with increasing latitude in South America is due principally to the increase in intra-annual temperature variation and the decrease in the minimum winter temperature (Farji-Brener & Ruggiero, 1994). Very high or low temperatures and humidity affect the leaf-cutting ants by limiting foraging activity (Gamboa, 1976; Mintzer, 1979) and by imposing a strong selective pressure on the construction of special structures that enable them to maintain an optimal microclimate for the fungus culture (Cherrett et al., 1989). Variations in such conditions can cause the death or reduction of the fungus, and with the loss of its principal food source, the ant colony is likely to die (Powel & Stradling, 1986). Therefore, leaf-cutting ants regulate the temperature of the fungus gardens by opening or closing entrances to the nest or by modifying the culture's location inside the nest during different times of the year (Na-

varro & Jaffe, 1985; Cherrett et al., 1989). Nest mounds, defined as a symmetrically shaped pile of excavated soil perforated with a dense system of interconnected galleries and often thatched with dry plant materials, are long known to play an important role in maintaining a suitable microclimate in numerous ant species (see Hölldobler & Wilson, 1990, p. 373, Bristow et al., 1992, and references cited in both texts).

Northern Patagonia is the climatically most rigorous environment that leaf-cutting ants have colonized. The mound-building *Acromyrmex lobicornis* Emery is the only leaf-cutting ant inhabiting this region, reaching 44°S latitude (Kusnezov, 1978; Farji-Brener & Ruggiero, 1994). *A. lobicornis* nests have an external sub-conical mound, about 80 cm high and 100 cm in diameter. This mound houses either one large, irregularly shaped fungus-garden chamber or a series of smaller ones located at surface level inside the mound or between 10–50 cm in depth (Bonetto, 1959; Weber, 1982; Fig. 1). In the Patagonian steppe where this leaf-cutting ant species is common, the patchy vegetation determines two types of *A. lobicornis* mounds: those constructed on bare soil

and those at the base of tussock plants, where the stalks form part of the nest structure (Fig. 1). Recently, *A. lobicornis* has amplified its geographic range towards the inhabited southwestern parts of the steppe by accompanying road borders, where nests frequently suffer anthropogenic disturbances that rupture the mounds (Farji-Brener, 1996) and which may lead to death of the colony or nest abandonment (Hölldobler & Wilson, 1990).

This study was aimed to investigate the importance of nest-mounds of *Acromyrmex lobicornis* in the colonization of temperate NW Patagonia, by (1) recording temperature variations inside and outside nest-mounds, (2) correlating nest architecture and damage to mounds to the death of the colony or the abandonment of the nests and (3) by analyzing, using the existing literature on the geographical ranges and distribution limits of different *Acromyrmex* species, whether the construction of mounds is correlated with more southerly distribution range. Additionally, I report basic information on density and mortality rate of nests of the only leaf-cutting ant in Patagonia, which is probably in the process of expanding its range and is considered a potential economic pest (Farji-Brener, 1996).

MATERIALS AND METHODS

Study site

The study was conducted in the eastern part of Nahuel Huapi National Park, 40 km north of San Carlos de Bariloche, NW Patagonia, Argentina (41° 07′S, 71° 13′W). Average annual precipitation in this area is 600 mm, falling mostly during the winter months (July–August). Mean annual temperature is 8°C, mean minimum in July is –2°C, and mean maximum in January is 23°C. Absolute temperatures can vary between –12°C and 37°C. Sampling was conducted along a road in a herbaceous-shrubby steppe, evidently altered by road maintenance and occasional human activities (Farji-Brener, 1996). Tussock plants dominate the patchy vegetation, principally by the grass *Stipa speciosa*, and by forbs and small shrubs generally less than 1 m in height (*Acaena splendens, Baccharis pingraea, Carduus nutans, Fabiana imbricata, Marrubium vulgare, Mulinum spinosum, Onopordium acanthium* and *Verbascum thapsus*) interspersed with areas of bare ground.

Measurements of environmental and nest temperatures

To analyze temperature differences inside the mound in relation to external temperatures, in five nests (70–100 cm of diameter) the temperatures in the fungus-garden chamber, the surface of the soil next to the mound and of the air at 15 cm above the nest were measured every hour from 8 to 18 h. The location of the fungus-garden inside the ant-mound was previously located by opening other nest mounds. Therefore, in the selected mounds temperatures were recorded with a digital thermocouple thermometer (Atkins® 396 series) without further disturbance. These measurements were taken on 5 days in spring, the season that exhibits the greatest daily thermal variations. To determine if the temperature of the interior of the dome possessed intermediate values in respect to the air and the surface of the soil, I used a Sign test, and a test that compares coefficients of variation (Zar, 1984) to analyze the daily variation between the three temperatures.

Mortality of colonies and growth of nest-mounds

To determine the mortality rate of nests and growth of nest-mounds in relation to the status and architecture of the mound, I conducted annual surveys over two years of 85 *A. lobicornis* nests. In May 1995 (before the winter), 43 active adult nests of *A. lobicornis* (>50 cm diameter) in an area of 15,000 m^2 were marked, recording the following characteristics of each mound: architecture (built on bare soil or on plants, Fig. 1), average diameter (measured in cardinal and intercardinal directions), and structure (intact or damaged). Nests were determined as active by the presence of ants foraging or working on the mound, and by the presence of fresh refuse on the soil surface near the nest (Claver, 1990). During May 1996 nests that had been marked in 1995 were inspected to verify if the nest continued to be active or not. Nest-mounds showing no activity during the entire survey period were considered abandoned or dead. In May 1996 a new sector of 5,000 m^2 with 19 active nests was incorporated and inspected in the new series of surveys of May 1997. As a result, the mortality of nests was estimated on observations made in two consecutive periods of 12 months each (95/96 and 96/97). Data were analyzed using contingency tables (χ^2 with Yates correction or Fischer exact test).
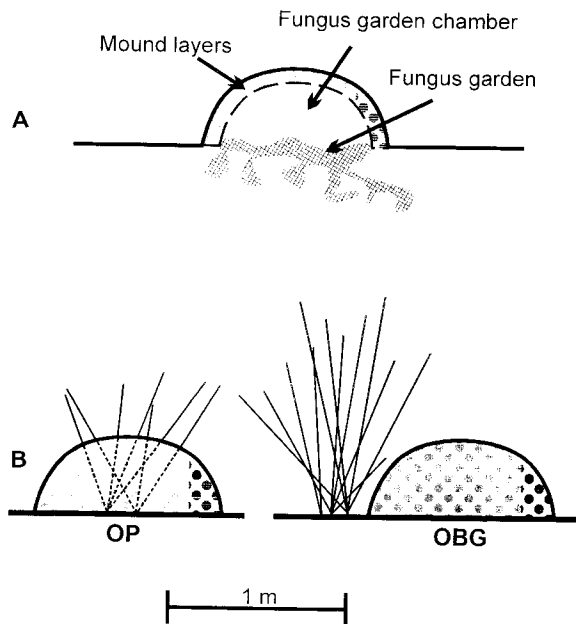
Fig. 1. Schematic view of *Acromyrmex lobicornis* nests-mound showing position of (A) the fungus-gardens, and (B) the two different types of mound architecture. OP = built on the base of tussock plants with the stalks forming part of the mound structure. OBG= mound built on bare ground.

Fig. 2. Within daytime variation of the temperature (mean ± SD) in the spring season inside the fungus-garden chamber of *Acromyrmex lobicornis* mounds, the nearby soil surface and the air at 5 cm.

Distribution of colonies

To determine if adult nests are located at random in relation to the two possible substrates (bare soil or surrounding the base of a plant). I marked 150 random points in the same area where the nests were located. Then I determined if the location of the nests was independent of the location of the random points using a χ^2 test.

Latitudinal range of Acromyrmex species

To relate the location and latitudinal extent of *Acromyrmex* spp. geographical range with the characteristics of their nests. I reviewed the existing literature on each species.

RESULTS

Range of environmental and nest temperatures

The temperature in the fungus garden-chamber within the mound fluctuated less than in the air and on the soil surface, and on average was warmer than the air and colder than the soil surface (Fig. 2. Sign test. $P < 0.01$). Wh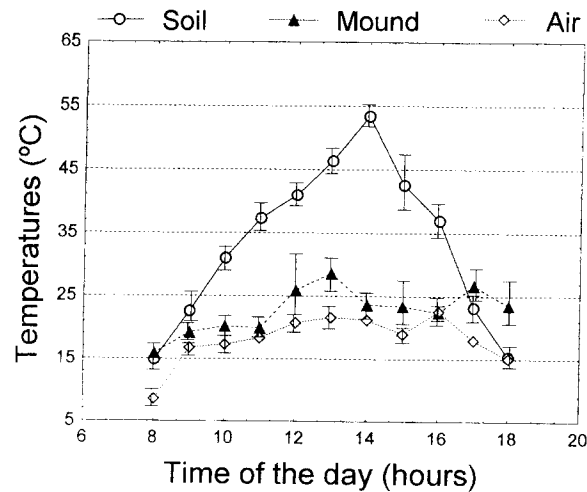ile the temperatures of the air and soil were strongly associated ($R_s = 0.84$, $P = 0.001$), those of the mound were relatively independent of the external temperatures ($R_s = 0.54$, $P = 0.08$ in both comparisons). In addition, the within daytime thermal variation inside the mound was less than that of the air and the soil (Coefficient of Variation 0.16, 0.21 and 0.39 respectively, $P < 0.05$, Fig. 2).

General characteristics and growth of mounds

During the study period I found 85 nests of *A. lobicornis* ($\approx$ 43 nests/ha), which were built on bare ground (OBG) and surrounding the base of a plant (OP) with about equal frequency. The species of plants on which mounds were most frequently built were the dominant *Stipa speciosa* and *Marrubium vulgare*, neither of which form an important part of the ants' diet (Farji-Brener, unpublished data). The nests constructed on plants did not differ in diameter from those constructed on bare ground, but grew larger during the study period (Table 1). The net increase in diameter of the mounds between 1995 and 1997 was negatively related with the diameter of the mound at the beginning of 1995 only for the nests constructed on plants ($Rs_{OP} = -0.48$, $P = 0.03$; $Rs_{OBG} = -0.27$, $P = 0.21$, Fig. 3). On the other hand, the location of the random points on possible substrates (bare ground or on plants) did not differ from the location of the nest-mounds for both nest-mound types ($\chi2 = 0.96$, $P > 0.95$).

TABLE 1. Increase of nest mounds in *Acromyrmex lobicornis* in NW Patagonia.

| | Mounds constructed on | | | | | |
| | Plants | | Bare ground | | | |
	$\bar{x}$	SD	$\bar{x}$	SD	t	P
Diameter (cm) (Range)	78.5 (35–105)	20.3	91 (60–135)	20	1.7	0.10
Increment (cm/2 years)	11	23	0.5	15	2.0	0.05

TABLE 2. Number of active colonies of *Acromyrmex lobicornis* in relation to nest architecture and condition of the mound in NW Patagonia between 1995 and 1997.

| Nest location | Mound condition* | Active nests | | | | | |
| | | 1995 | 1996 | Mortality | 1996 | 1997 | Mortality |
		n	n	%	n	n	%
Bare ground	damaged	7	2	71.4	3	0	100
	intact	14	12	14.3	17	13	23.5
	subtotal	21	14	33.3	20	13	35
On plants	damaged	10	7	30	1	1	0
	intact	12	11	8.3	21	14	33.3
	subtotal	22	18	18.2	22	15	31.8
	Total	43	32	28	42	28	33.3

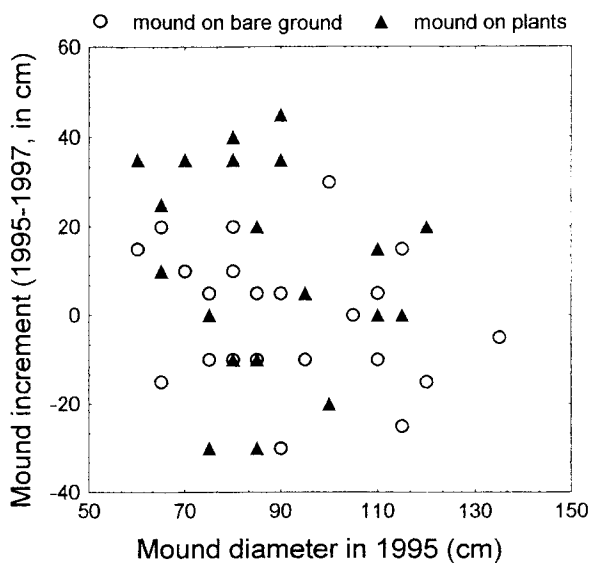(*) Condition of the mound in the first year of each sample period (1995 and 1996 respectively)

Fig. 3. Relationship between the diameter of *Acromyrmex lobicornis* mounds built on bare ground (OBG) and on plants (OP) in 1995 and their increment during the sample period (95/97). Rs $_{OP}$ = -0.48, P = 0.03, Rs $_{OBG}$ = -0.27, P = 0.21).

Colony mortality

In both years (95/96 and 96/97), the abandonment of nests or death of colonies was strongly associated with the presence of damages in the mound built on bare ground only (95/96: P_{OBG} = 0.017, P_{OP} = 0.29; and 96/97: P_{OBG} = 0.03, P_{OP} = 1.0, Fisher exact tests, Table 2). Grouping the two-year sample periods, the adult colonies of *A. lobicornis* were characterized by a 32% death or nest abandonment rate and a 68% survival rate.

Although the occurrence of breaks was independent of the type of mounds ($\chi2$ = 0.25, P = 0.62 in 1996, $\chi2$ = 0.39, P = 0.53 in 1997, Table 2), the survivorship of these broken mounds was related with the type of mound. Mortality of damaged nests built on bare ground was higher than of those nests built on plants. In the sampling period 95/96, damaged nests on bare ground showed 28.6% survivorship, whereas those on shrubs showed 70% survivorship (P = 0.03, Fisher exact test, Table 2). Between

1996 and 1997, none of the damaged nests on bare ground survived, but the only broken mound located on plants remained active (P < 0.001, Fisher exact test, Table 2). Breaks in mounds were most often produced by horses and humans (in approximately 90% of the cases tracks could be seen), and less frequently without apparent external cause.

Latitudinal range of *Acromyrmex* spp.

For species of *Acromyrmex* that construct mounds, a more southerly mean geographic range and geographical limits at higher latitudes were calculated than for those species that do not construct mounds (t = 2.8, P = 0.02, Table 3 and Table 4). Of the 24 species of *Acromyrmex* cited in Hölldobler and Wilson (1990) and Cherrett (1989), 6 were excluded from the analysis due to uncertain information regarding type of nest, taxonomic status, and/or geographic distribution (Table 3). Eight of the remaining species are described as having subterraneous fungus-culture chambers without mounds, while the oth-

er are characterized as having more superficial culture chambers with mounds. These 10 were grouped together in spite of the fact that in some of these species the presence of the mound depends on the subspecies or the environment.

DISCUSSION

Nest temperature, environmental conditions and the role of mound for thermoregulation

Even though temperatures in and outside the nest were measured only in spring, the buffering effect of the mounds on the range of temperature variability within the fungus-chamber of *A. lobicornis* is obvious. The average temperature of 23 C inside the mounds observed here is similar to that found in mounds of *A. lobicornis* in Uruguay (Zolessi & Gonzalez, 1974) and is within the optimal range for fungus growth as reported in other Attini ants (Powel & Stradling, 1986; Hölldobler & Wilson, 1990) indi-

TABLE 3. Relation between nest structure and geographical range in leaf-cutting ants of the genus *Acromyrmex*. + = mound present, − = mound absent.

Species	Latitudinal range	Mound present	Fungus substrate
Subgenus *Moellerius* Forel, 1893			
A. heyeri Forel	18°–36°S	+	G
A. landolti Forel	10°N–32°S	−	G
A. striatus Roger	20°–35°S	−	G/D
Subgenus *Acromyrmex* Mayr, 1865			
A. ambiguus Emery	18°–38°S	+ (*)	D
A. coronatus Fabricius	10°–27°S	+ (*)	D
A. crassispinus Forel	22°–30°S	+	D
A. diasi Gonçalves	13°–15°S	−	G
A. disciger Mayr	20°–30°S	+ (*)	D
A. hispidus Santschi	10°N–30°S	+ (*)	D
A. hystrix Latreille	10°N–2°S	−	D
A. laticeps Emery	0°–32°S	+	D
A. lobicornis Emery	18°–44°S	+	G/D
A. lundi Guerin	18–37°S	+ (*)	G/D
A. niger Fr. Smith	22°–24°S	−	D
A. nobilis Santschi	2°N–8°S		D
A. octospinosus Reich	22°N–3°S	−	D
A. rugosus Fr. Smith	0°–32°S	−	D
A. subterraneus Forel	0°–30°S	+	D

(*) = not all authors report presence of mounds. It is possible that the mound exists only in some subspecies or habitats. G= Gramineae. D= Dicotyledones.

Major sources of data: Bonetto, 1959; Gonçalves, 1961; Kusnezov, 1978; Zolessi & Gonzalez, 1974; Fowler & Robinson, 1979; Fowler et al., 1986b; Fowler & Claver ,1991; Della-Lucia & Moreira, 1993; Farji-Brener & Ruggiero, 1994; Farji-Brener, 1996; and Verhaagh et al. pers. comm.

List of species with doubtful information or uncertain taxonomical status that were excluded from the analysis: *Acromyrmex aspersus* Fr. Smith, *Acromyrmex gallardoi* Santschi, *Acromyrmex mesopotamicus* Gallardo, *Acromyrmex pulverens* Santschi, *Acromyrmex silvestrii* Emery, and *Acromyrmex versicolor* Pergande.

TABLE 4. Presence of nest mounds and southerly geographic distribution in leaf-cutting ants of the genus *Acromyrmex*.

	Latitude range	Southern limit	
		$\bar{x}$	SE
with mound	10°N–44°S	33.4	2°
without mound	22°N–35°S	13.6	5°

cating the vital importance of this nest structure on colony survival of these leaf cutting ants exposed to extremely high daily and annual temperature differences. In fact, true mounds are most commonly found in habitats subject to extreme temperatures (Hölldobler & Wilson, 1990).

Regulation of microclimate within ant nests by shifting of nest material and rearrangement of shape and internal structure is a common phenomenon in tropical as well as in temperate latitudes, and has also been observed in leaf-cutting ants. The low surface/volume ratio of the semi-spherical mound minimizes the thermal interchange with the exterior. When the shape is altered experimentally, the ants rapidly restore the original form (Hölldobler & Wilson, 1990, and personal observations). The mound of *A. lobicornis* is composed of 2 to 4 superimposed layers, connected by galleries to the central fungus gardens (Zolessi & Gonzalez, 1974). The ants' capacity to adapt to temperate environments is, in part, related to their ability to modify the number and disposition of the layers of its mounds, which lessens the negative effects of external climatic variations on fungus growth (Zolessi & Gonzalez, 1974; Della-Lucia & Moreira, 1993). The breakage of this complex structure can be catastrophic for the colony, especially in temperate environments, because it may cause an abrupt thermal imbalance inside the nest. When severe disturbances allow air and light to penetrate the fungus gardens and/or the brood chambers, the colony dies or abandons the nest in order to construct a new one (Fowler, 1981; Hölldobler & Wilson, 1990).

Influences of nest architecture and damage on colony survival

The presence of plant stems in the mound seems to facilitate the response of *A. lobicornis* to external perturbations. In the study area the disturbances harm equally the mounds constructed on bare ground or on

plants. Nevertheless, nest abandonment or death of colonies over a 2-year period was significantly associated with previous damages to the mound only for the nests built on bare ground. The majority of the nests characterized as abandoned at the end of the period showed signs of mound damage, but it was difficult to determine if the damage was a cause or a consequence of abandonment (i.e., mound structure collapsed because it was no longer maintained by the ants). Given that breaks in mounds had occurred between sampling periods, it is perhaps more important to point out that the survival rate after damage to the mound is significantly greater for nests built on plants. If the mound is an important structure for colony survival, colony transfer to a new nest site should only occur when the 'costs' of the repair exceeds the 'costs' of the move and construction of a new nest-mound. Here the presence of plant stems in the mound seems to decrease the 'cost' of the repair, perhaps by improved stability and easier repair of the different layers of the mounds.

For the same reason, the presence of stems in the mound seems to speed up nest construction during the early stages of the colony, especially for mounds less than 90 cm in diameter. Therefore, differences in growth rates between the two types of nests should be considered when using nest volume as an indicator of age and/or biomass of the colony (see Fowler et al., 1986a; Tschinkel et al., 1995).

Even though building a mound on a plant has an advantage for *A. lobicornis*, the proportion of the two types of nest is similar to that of the availability of the respective sites (bare ground or plants) suggesting that the queens show no preferences for plants when founding a new colony. However, in some leaf-cutting ants species microhabitat preferences of founding queens have been reported (Navarro & Jaffe; 1985, Fowler, 1987; Vasconcelos, 1990). Therefore, further observations of *A. lobicornis* should be made during the nest founding stage to determine if habitat selection does exist, the scale at which it could occur, and if such behavior is inheritable and thus subject to selection.

Given the great capacity for nest movement of *Acromyrmex* species in general ('emigration specialist' *sensu* Fowler, 1981) and *A. lobicornis* in particular (Zolessi & Gonzalez, 1974; Claver, 1990), an inactive nest does not necessarily imply the death of the colony since the nest could have been abandoned. Most of the time it was difficult to determine the

status of the colony because continuous observation is needed. In addition, a new nest can be built at a great distance from the former (Fowler, 1981). Between 1995 and 1997, I observed 5 colonies of *A. lobicornis* emigrating and constructing new mounds, which implies that at least 10% of the colonies considered dead would be active. As a result, the mortality rate of *A. lobicornis* calculated in this work may be over-estimated. Nevertheless, the three-fold larger nest density that this species shows in the relatively disturbed study area in comparison to a similar but protected and undisturbed area in Mendoza Province, Argentina might indicate that *A. lobicornis* is well-adapted to modified environments (Claver, 1990). This plasticity towards disturbances (mound repair or relocation of nest) could be one reason why this species is such an excellent colonizer of semi-urban and cultivated areas. (Kusnezov, 1953, 1978; Bonetto, 1959; Zolessi & Gonzalez, 1974; Farji-Brener, 1996).

Correlation between mound building and geographical distribution

The fact that, on a large scale, more mound-building *Acromyrmex* species occur farther south than species without mounds suggests that its function in thermoregulation might be one important trait for range expansion towards subtropical and even temperate environments. Nevertheless, this result must be considered with caution since species might not be regarded as statistically independent 'sampling units', limiting the evolutionary interpretations of the presence of the mound (see Harvey & Pagel, 1991). In spite of this, it is noteworthy that this pattern manifests independently of the subgenus and fungus substrate, and that species of *Acromyrmex* with mounds principally occupy such biomes in South America characterized by great daily and/or seasonal climatic variations (see Hueck, 1978), e.g., the dry forests of the central Chaco, the prairies and shrub steppes of the Monte region, and the steppes and semi-deserts of Patagonia. (Gonçalves, 1961; Kusnezov, 1978; Farji-Brener & Ruggiero, 1994).

Conclusions

Three lines of evidence suggest that for ants in the genus *Acromyrmex*, mounds play an important role in the colonization process of temperate habitats: (1) the mounds function as 'thermal buffers' by diminishing the effects of external temperature changes,

(2) damages to the mound increase the probability that the colony will die or abandon the nest, and (3) mound building *Acromyrmex* species have more southerly latitudinal extensions than those without mounds.

ACKNOWLEDGMENTS

REFERENCES

Bonetto A (1959): *Las Hormigas Cortadoras de la Provincia de Santa Fe (Atta & Acromyrmex)*. Min. de Agricultura y Ganadería, Provincia de Santa Fe. República Argentina.

Bristow C, Cappaert D, Campbell N, Heise A (1992): Nest structure and colony cycle of the allegheny mound ant *Formica exsectoides* (Hymenoptera: Formicidae). *Insectes Soc 39*: 385–402.

Cherrett M (1989): Leaf-cutting ants, biogeographical and ecological studies. In: Lieth H, Werger D, eds., *Ecosystems of the World 14b, Tropical Rain Forests*. Elsevier. N. Y., pp. 473–488.

Cherrett JM, Powell RJ, Stradling DJ (1989): The mutualism between leaf-cutting ants and their fungus. In: Wilding N, Collins N, Webber J, eds., *Insect-Fungus Interactions*. Academic Press, London, pp. 93–120.

Claver S (1990). Methods for estimating the population density of leaf-cutting ant colonies. In: Vandermeer R, Jaffe K, Cedeño A, eds., *Applied Myrmecology: A World Perspective*, Westview studies in insect biology, Boulder, pp. 220–227.

Coutinho LM (1982): Aspectos ecológicos da saúva no cerrado: os murundus da terra, as características psamofíticas das espécies da sua vegetação e a sua invasão pelo capim gordura. *Revta Brasil Biol 42*: 147–153.

Della-Lucia TM, Moreira D (1993): Caracterização dos ninhos. In: Della-Lucia TM. ed., *As Formigas Cortadeiras*, Editora folha de Viçosa, Viçosa, Brasil, pp. 32–42.

Farji-Brener AG (1996): Posibles vías de expansión de la hormiga cortadora de hojas *Acromyrmex lobicornis* hacia la patagonia. *Ecología Austral 6*: 144–150.

Farji-Brener AG, Ruggiero A (1994): Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: Patterns in species richness and geographical range sizes. *J Biog 21*: 535–43.

Farji-Brener AG, Margutti L (1997): Patterns of plant species in relation to *Acromyrmex lobicornis* nest-mounds on roadside vegetation in northwest Patagonia. *Int J Ecol & Env Sci 23*: 37–47.

Fowler H (1981): On the emigration of leaf-cutting ant colonies. *Biotropica 13*: 316

Fowler H (1987): Colonization patterns of the leaf-cutting ant *Atta bisphaerica* Forel: evidence for population regulation. *J Appl Ent 104*: 102–105.

Fowler H, Robinson S (1979): Field identification and relative pest status of Paraguayan leaf-cutting ants. *Turrialba 29*: 11–16

Fowler H, Forti L, Da-Silva V, Saes N (1986a): Population dynamics of leaf-cutting ants. In: Logfren S, Vandermeer R, eds., *Fire and Leaf-cutting Ants: Biology and Management*, Westview Press, Boulder, Colorado, pp. 123–145.

Fowler H, Forti L, Da-Silva V, Saes N (1986b): Economics of gran-cutting ants. In: Logfren S, Vandermeer R, eds., *Fire and Leaf-cutting Ants: Biology and Management*, Westview Press, Boulder, Colorado, pp. 18–35.

Fowler H, Claver S (1991): Leaf-cutter ant assemblies: effects of latitude, vegetation and behaviour. In: Huxley CR, Cutler DF, eds., *Ant-Plant Interactions*, Oxford Univ. Press, Oxford, pp. 51–59.

Gamboa G (1976): Effects of temperature on the surface activity of the desert leaf-cutting ant *Acromyrmex versicolor*. *Am Midl Nat 95*: 485–491.

Gonçalves C (1961): O genero *Acromyrmex* no Brasil (Hym. Formicidae). *Studia Ent, Vol 4, Fasc. 1–4*: 113–180.

Harvey P, Pagel M (1991): *The Comparative Method in Evolutionary Biology*, Oxford Univ. Press, London.

Hölldobler B, Wilson EO (1990): *The Ants*, Harvard Univ. Press, Cambridge, Massachusetts, 732 pp.

Hueck K (1978): *Los Bosques en Sudamérica. Ecología, Composición e Importancia Económica*, República Federal Alemana. Soc. Alemana de Cooperación Técnica.

Kusnezov N (1953): *Las Hormigas de los Parques Nacionales de la Patagonia y los Problemas Relacionados*, Anales del Museo Nahuel Huapi, Tomo III, Buenos Aires, Argentina, pp. 105–125.

Kusnezov N (1978): *Hormigas Argentinas: Claves para su Identificación*. Miscelanea 61, Tucuman, Argentina.

Mintzer A (1979): Foraging activity of the Mexican leaf-cutting ant, *Atta mexicana* in a Sonoran desert habitat. *Insec Soc 26*: 364–372.

Navarro J, Jaffé K (1985): On the adaptive value of nest features in the grass-cutting ant *Acromyrmex landolti*. *Biotropica 17*: 347–348.

Powell RJ, Stradling DJ (1986): Factors influencing the growth of *Attamycetes bromatificus*, a symbiont of Attine ants. *Trans Br Mycol Soc 87*: 205–213.

Smalwood J, Culver D (1977): Colony movements of some North American ants. *J Anim Ecol 48*: 373–382.

Tschinkel WE, Adams E, Macom T (1995): Territory area and colony size in the fire ant *Solenopsis invicta*. *J Anim Ecol 64*: 473–480.

Vasconcelos H (1990): Habitat selection by the queens of the leaf-cutting ant *Atta sexdens* L. in Brazil. *J Trop Ecol 6*: 249–252.

Weber A (1982): Fungus ants. In: Hermann H, ed., *Social Insects*. Vol. 4, Academic Press, London, pp. 255–363.

Zar J (1984): *Biostatistical Analysis*. Second edition. Prentice-Hall, N. J.

Zolessi LC, González LA (1974): Nidificación y mesoecología de *Acromyrmex* en Uruguay: II *Acromyrmex lobicornis* (Hymenoptera: Formicidae). *Rvta Biol Urug 1*: 37–57.