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Some factors influencing colony spacing and survival in the grass-cutting ant Acromyrmex landolti fracticornis (Forel) (Formicidae: Attini) in Paraguay

by

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Abstract: Various aspects of the ecology of the Paraguayan grass-cutting ant, *Acromyrmex landolti fracticornis* (Forel), were studied in the field. Colonies were found to linearly orient their foraging territories, partitioning the habitat in a mosaic pattern. The distances foraged by workers were found to be a function of colony size: (Log_{10} maximum distance foraged) = -0.5156 + 0.4121 (Log_{10} area of nest). Colony spacing, however, was found to be not immediately dependent on colony size. Colony spacing patterns are influenced by intra-specific aggression, and perhaps by the predation or execution of founding queens. Both the mound and superficial detritus heap of nests were found to favor the survivorship of forbs. Colony numbers were found to decrease significantly as grass coverage decreased and forb species became dominant.

Leaf-cutting ants of the genera *Atta* and *Acromyrmex* are important herbivores of the neotropics (**Weber,** 1972). **Wheeler** (1907) considered them to be the "dominant" invertebrates of those areas in which they occur. The genus *Acromyrmex* has been shown to be "dominant" in terms of its numerical abundance (**Kusnezov,** 1963), while indirect evidence exists that *Acromyrmex landolti fracticornis* (Forel) may be "dominant" by regulating the grazing of other invertebrates (**Fowler & Robinson,** 1977). However, factors governing the spatial distribution of leaf-cutting ant colonies are not well understood.

Wilson (1971) considered that colony spacing in ants may be achieved through inter- and intra-specific aggression between mature queens, and by the execution of founding queens by established colonies. In leaf-cutting ants, colony displacement also serves as spacing mechanism (**Rockwood,** 1973). As leaf-cutting ants may employ a conservational foraging strategy (**Cherrett,** 1968; **Rockwood,** 1975), spacing mechanisms should maximize long-term resource exploitation.

The relationships between leaf-cutting ants and vegetation have been studied

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from the standpoint of the ants' exploitation of plants (**Cherrett,** 1968; **Rockwood,** 1975). The nest maintenance activities of some species of leaf-cutting ants are well known to influence vegetational patterns (**Bucher & Zuccardi,** 1967; **Haines,** 1971; **Jonkman,** 1976).

This paper presents data on the grass-cutting *A. landolti fracticornis* (Forel), a dominant component of Paraguayan range lands (**Fowler,** 1977a). Foraging territories, intraspecific relations, aggression, and ant-plant interactions are examined, and their relative importance to colony spacing is discussed.

METHODS

Ant-ant interactions: In March, 1975, the following data were recorded for each nest in a 100 m^2 plot of grasses near Asunción, Paraguay: (a) the number of nest entrances; (b) the maximum height of the mound; (c) the distance between the nearest colonies, as measured between entrance holes; and (d) the vegetative cover of the mound, recorded as classes: 1 = 0 - 20%; 2 = 21 - 40%; 3 = 41 - 60%; 4 = 61 - 80%; 5 = 81 - 100%. Factors (a), (b), and (d) were used as an index of colony size to determine their effect on colony spacing.

Foraging territories were studied in a 30 m^2 sub-plot of the same plot in September, 1975. Foragers were aspirated into vials as they left their colonies, and were then cooled on ice until motionless. The ants were then marked with paint on the dorsal surface of the gaster, with a distinctive color or color combination used for individuals of different colonies. A minimum of 20 workers from each colony were marked over a 2 day period. During the next five days, the area was searched carefully for marked ants, whose location was then recorded on a reference map to determine the ranges of their foraging activity.

Behavioral observations from more than 500 hr of field observation over a one-year period (**Fowler & Robinson,** 1975) are also included.

Ant-vegetation interactions: In February, 1975, the number of nests was recorded for two 100 m^2 plots of Bermuda grass, *(Cynodon dactylon)*. At the same time, the percentage of grass cover was estimated for each plot using the loop method (**Parker,** 1954), which was modified for small plots. A 2 cm diameter wire loop was placed to the right of the 10, 30, 60 and 90 cm points of each meter of a 10 m tape, and the percentage cover was estimated for each reading. In all, 100 loop readings were taken for each plot. The grass coverage was taken as the mean percentage cover of the summed individual loop readings.

To determine the effects of pasture management on nest densities, one plot was left untouched to allow vegetational succession to proceed, while the other plot was cut monthly to retain a fairly high and uniform grass stand. A year later, nest densities and grass coverage were reassessed. In May, 1975, the numbers and heights of forb seedlings per m^2 were determined for open ground, the nest mound surface, and the superficial detritus heap, the latter being formed of exhausted material accumulated to one side of the nest. These measurements were taken in the naturally succeeding plot.

RESULTS

Colony size and spacing: The significant positive correlations found between the number of nest entrances, the height of the mound, and the percentage of vegetational cover tends to indicate that all three may be valid indexes of colony size (Table 1). If high values of these are assumed to indicate older colonies, and low values young colonies, then no significant relation was found between colony size and the distance to the nearest colony (Table 1).

Physical relations of Acromyrmex landolti fracticornis *nests and colony spacing (correlation coefficients) based on measurements of 65 nests*

	Surface area	Nº of entrances	Max. height	%vegetative cover	Nearest nest (cm)
Surface area	–	0.770*	0.648*	0.258*	0.032
Nº of entrances	–	–	0.739*	0.305*	-0.051
Max. height	–	–	–	0.165	0.082
%vegetative cover	–	–	–	–	0.119

* $P < 0.05$

Foraging territories and colony densities: The pooled totals for the two plots gave 117 nests/200 m^2, or an equivalent 5,850 nests/ha. As this value was quite high, a detailed, short-term study of the foraging territories was undertaken to determine if overlap of foraging territories was minimized.

From behavioral observations, foraging territories were thought to be linear. The results of the marking experiments showed this to be true over a short term and the habitat was partitioned in a mosaic pattern (Fig. 1). The mean length of the foraging territories of the individual colonies was 1.03 m ($s = 7.17$). However, during the period of study not all the habitat was being exploited, although it was assumed that these foraging territories would change somewhat with time. More significantly, foraging territories were found to orient away from the superficial detritus heap (Fig. 1).

The distance of furthest sighting of marked foragers was also found to increase with colony size. The equation (Log_{10} maximum observed cutting distance) $= -0.5156 + 0.4121$ (Log_{10} area of nest surface) accounted for 92% of the variation. Ants from larger nests forage farther than ants from smaller nests, often by displacement of the former's foraging territories, while smaller colonies tend to forage closer to their nests.

Intra-specific aggression: During 500 hs of observation, aggression between colonies was seen on 5 occasions, and each time occurred on or near a nest mound. During aggression, a higher than normal number of workers was seen on the surface, but actual aggressive contacts were few. Mutual avoidance between workers of different colonies was common. Aggression lasted from 3 to 6 hr. Four of the five attacked colonies lived as long as six months following aggression. In the fifth however, the attacking workers were seen entering the nest of the attacked colony, and were later observed transporting larvae and pupae to their own nest and 15 days later no activity was observed in the attacked nest. Aggression was never seen occurring away from the nest surface. However, joint use of foraging trails was observed (Fig. 1), suggesting that only the nest itself is physically protected.

Foraging by founding queens: Incipient queens were observed foraging on four occasions in January, 1976. All were followed to their freshly excavated chambers and then collected. All chambers were excavated, revealing small (0.2 cm) fungus gardens in which small pieces of grass were visible, small egg masses were also present in each chamber.

TABLE 2

Annual change in vegetative cover and Acromyrmex landolti fracticornis *nest numbers in naturally succeeding and artificially grazed pastures*

	% grass cover		Colony numbers/100 m^2	
Date	Natural succession	Artificially grazed	Natural succession	Artificially grazed
II/ 1975	62.8	68.7	65	52
II/ 1976	11.4	73.2	27	46
	X^2 26.834		X^2 5.479	
	$P \leq$ 0.001		$P \leq$ 0.02	

Ant-vegetation relations: When allowed to proceed a natural successional course, a significant decrease in grass coverage occurred at the end of a year (Table 2). Forb coverage, though not measured, likewise increased in this plot. The managed plot remained practically unchanged (Table 2).

The nesting activities of *A. l. fracticornis* were found to influence forb survivorship. When forb heights are plotted against forb numbers, assuming height to be proportional with age, both the nest mound and the superficial detritus heap were found to greatly influence forb survival (Fig. 2). Although more forbs were found in undisturbed ground, a higher percentage of the forbs on the nest mound and superficial detritus heap attained greater height.

The reduction of colony numbers after one year in the naturally succeeding plot was significant (*P* 0.02) (Table 2). Although colony numbers also dropped in the artificially maintained plot, these were not significant.

DISCUSSION

In species of *Atta,* colony age, and therefore populations, can be estimated by external nest characteristics (**Bitancourt,** 1941). Data presented here suggested that this may also be true of *A. l. fracticornis.* However, the data suggest no relationship between colony size and colony spacing. Nevertheless, the distance foraged by workers of *A. l. fracticornis* increases with increasing colony size, as is also true for *Atta cephalotes* (L.) (**Lewis** et al., 1974).

The foraging territories observed were linear, which differs them from the foraging territories of other grass-cutting, range-dwelling ants. Foraging territories of *Atta capiguara, Atta vollenweideri, Atta laevigata, Acromyrmex heyeri* and *Acromyrmex lundi* are approximately circular (unpub. pers. observ.), as is probably true for tropical forest species. This linear orientation of foraging territories of *A. l. fracticornis* may be attributable to minimizing territorial overlap and thus reducing competition. However, solitary colonies were also found to forage along a linear orientation, and thus would appear to be species-specific behavior.

Even though joint utilization of foraging trails and territories was observed, this behavior is rare. **Elton** (1932), **Brian** *et al.* (1965) and **Wilson** *et al.,* (1971) have shown that some ant species maintain separate foraging territories, which is also the general rule for *A. l. fracticornis.* However, *A. l. fracticornis* was not observed to physically defend these territories, although these may be maintained by chemical or other means.

As aggression was observed 5 times during approximately 500 hr of observation, or one aggressive contact/100 hr, this may be important in regulating colony populations or foraging territories. Intra-specific aggression is common in *Atta sexdens* (**Autuori,** 1941; **Mariconi,** 1970) and also occurs in *Atta colombica* (**Rockwood,** 1973). Intra- and inter-specific aggression may determine, in part, spacing patterns of leaf-cutting ant colonies (**Rockwood,** 1973). The theft of brood and subsequent colony death in one observed aggressive encounter, lend added support to this theory. Brood theft also occurs in laboratory colonies of *Acromyrmex octospinosus* (S. W. Robinson, pers. comm.). This may help to explain why only the nest itself is defended, which is also true for *Acromyrmex crassispinus* (**Fowler,** 1977b).

As *Acromyrmex* queens possess a complete repertory of species-specific behavioral acts (totipotency) (**Wilson,** 1971), foraging by incipient queens was to be expected. Foraging has previously been reported for incipient queens of *A. octospinosus* **(Cordero,** 1963), *A. hispidus* **(Weber,** 1972) and *A. striatus* **(Montenegro,** 1973); it also occurs in *A. rugosus* (unpub. pers. observ.). As **Montenegro** (1973) points out, foraging by founding queens increases their probability of predation, due to increased superficial exposure. This superficial exposure may also increase their chances of being executed by workers from near-by colonies. Conspecific execution of founding queens occurs in *A. colombica* **(Parker,** 1954), *A. capiguara* and *A. vollenweideri* (unpub. pers. observ.), and is probably a regulator of spacing patterns and colony densities.

The selective herbivory and nest maintenance activities of leaf-cutting ants have been thought to influence vegetational patterns. The detritus removal activities of *Atta cephalotes* increases seedling survival in tropical rain forests **(Haines,** 1971). The nesting activities of *A. vollenweideri* initially inhibit vegetational growth **(Bucher & Zuccardi,** 1967), but later serve as the focal points of woody plant growth in the savanna of the Paraguayan Chaco **(Jonkman,** 1976). **Tamayo** (1964) suggests that *A. landolti* may be responsible for shrub succession in Venezuelan range lands. It has been shown here that *A. l. fracticornis* influences forb survivorship, though it is difficult to assess its real importance.

The influence of vegetation on *A. l. fracticornis* is more clear-cut. As grass coverage significantly decreased, so did colony numbers. As the forb: grass balance is usually determined by grazing pressure, the reduction of grass coverage may have been due to competition with forbs in the naturally succeeding plot. As colony density is significantly correlated with basal grass coverage **(Fowler & Robinson,** 1977), a reduction of colony numbers was expected. This reduction may be the result of a shortage of available, harvestable substrate, which must meet certain physical and chemical specifications to be foraged by *A. l. fracticornis* **(Fowler & Robinson,** 1977).

RESUMEN

Algunos factores que afectan los patrones espaciales de las colonias de la hormiga gramnivora *Acromyrmex landolti fracticornis* (Forel) son considerados bajo condiciones naturales. La agresión entre colonias y, quizá, la ejecución de las reinas incipientes podrán tener mucha importancia. Los territorios de forrajeo se orientan linealmente, dividiendo los recursos disponibles en un mosaico. La distancia forrajeada por las hormigas es función del tamaño de la colonia. Las actividades del mantenimiento de la colonia, tales como la construcción del túmulo y la formación de un basurero superficial, afectan la supervivencia de malezas. Con la disminución de la cobertura de pastos y el aumento de la de malezas, las densidades de colonias decayeron significativamente.

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Fig. 1. Foraging territories of colonies of *Acromyrmex landolti fracticornis* in field near Asunción. Circle = mound, Star = detritus heap.

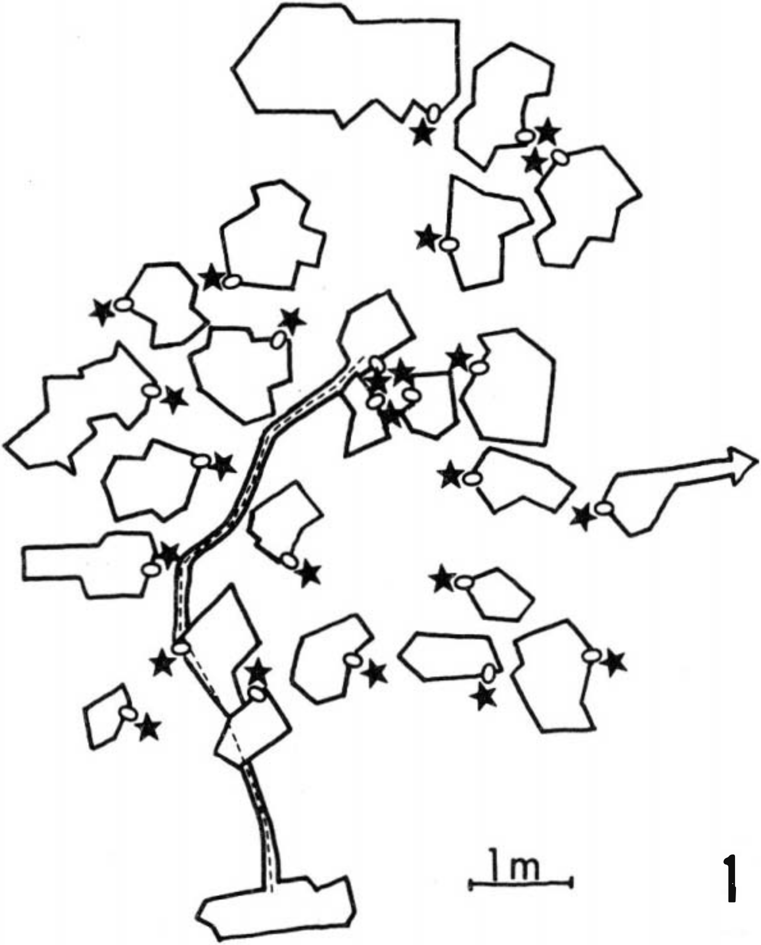

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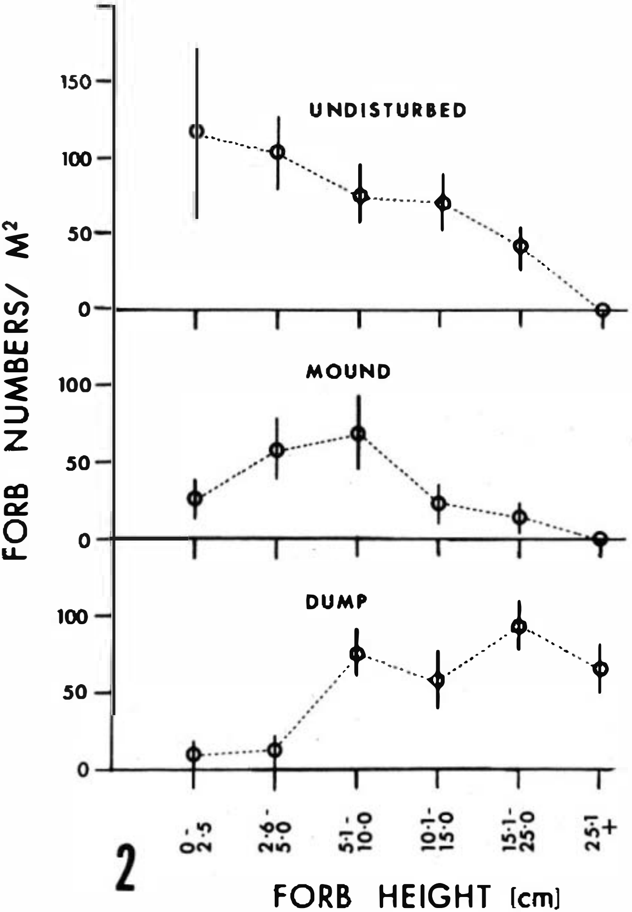
Fig. 2. Forb seedling survival on pasture, nest, and detritus heap. Seedling density is plotted against seedling height. Vertical lines show 95% confidence levels to means from 30 replicates.


FORB NUMBERS/ M²
UNDISTURBED
150
100
50
0
MOUND
100
50
0
DUMP
100
50
0
0-2·5
2·6-5·0
5·1-10·0
10·1-15·0
15·1-25·0
25·1+
FORB HEIGHT (cm)

2