

Field identification and relative pest status of Paraguayan leaf-cutting ants* ————— HAROLD G FOWLER**, S W ROBINSON***

COMPENDIO

*Se comparan dos métodos para la identificación de las especies paraguayas de hormigas cortadoras (géneros Atta y Acromyrmex). El empleo de una fórmula dise-
 ñada de análisis canónico permite distinguir entre las especies mejor que una clave
 tradicional. En ambos casos se utilizaron las características etológicas y ecológicas de
 las especies para distinguirlas. El uso del análisis canónico puede ser muy útil a ex-
 tensionistas para determinar el tipo de control apropiado para la especie en cuestión,
 sobre todo cuando no es posible identificar con exactitud la especie por falta de un
 taxónomo especializado. Se discute brevemente el estado de plaga de las especies.
 Aparentemente las especies de Atta son de mayor importancia que las especies de
 Acromyrmex en el Paraguay.*

Introduction

LEAF-CUTTING ants of the genera *Atta* and *Acromyrmex* are considered as the major pests of agriculture in Paraguay (1, 3, 4, 2, 5, 6). A previous survey (2) revealed that Paraguay is richly endowed with a complement of species of leaf-cutters, and a control scheme to develop a locally produced bait has produced favorable results (5). However, due to the lack of trained ant taxonomists within Paraguay, species identification is often impossible, especially for closely related forms. At the practical level, it would be highly desirable to understand how the behaviors and ecologies of the different species and subspecies relate to bait acceptability and control, and at this level, an accurate identification of the species in question is not essential.

Here we present two suitable methods for the field identification of the Paraguayan species of *Atta* and *Acromyrmex* based upon ecological and ethological variables that are easily ascertained by a trained extension agent. The first is a simple dichotomous key, which allows for the determination of the species in question in a traditional way. The second method is through canonical correlation analysis. Finally, we discuss the relative pest status of the species in question.

Materials and methods

Based upon data of the distribution (2), and the biology of the species and subspecies of *Atta* and *Acromyrmex* known to occur in Paraguay (2), data were assigned numeric values (Table 1). The simple dichotomous data were used to construct a field key, and the numeric values were used to run canonical correlations (7), through computer aided calculations. Worker sizes (the size of the major workers) was taken from Fowler (2).

Results

Field key to Paraguayan leaf-cutting ants

- 1—Nests small or not visible. Ants small; similar to *Acromyrmex* but lacking polymorphism. Ants cut little or no vegetation, and when they cut, they only take extremely small pieces. Colonies almost never reach pest status. *Lesser genera*
- Medium sized to large ants, with polymorphic forms. Ants cut vegetation, sometimes in quantities, and can become economic pests. *genera Atta and Acromyrmex* 2
- 2—Leaf cutting ants of forests, orchards, shrublands or crops 3
- Leaf cutting ants of grasslands or shrublands 12

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Table 1.—Behavioral and ecological attributes of Paraguayan species and subspecies of *Atta* and *Acromyrmex* and their relative pest status. Values in parenthesis are those used for canonical analysis

Criteria	Predict									Relative Pest status	
	Habitat	Foraging strategy	Substrate	Distribution	Nest type	Detritus disposal	Foraging trails	Foraging territory	Galleries	agriculture	ranching
(1) Genus <i>Acromyrmex</i>											
(1) Subgenus <i>Acromyrmex</i>											
(1) <i>ambiguus</i>	**	**	**	**	*	*	**	**	*	X	X
(2) <i>coronatus</i>	*	*	**	**	**	*	*	*	*	XX	—
(3) <i>crassispinus</i>	*	**	**	**	**	*	**	**	*	XX	—
(4) <i>disciger</i>	*	**	**	**	*	*	**	**	*	X	—
(5) <i>hispidus fallax</i>	**	**	**	**	**	*	*	**	*	X	X
(6) <i>laticeps laticeps</i>	**	**	**	**	**	*	**	**	*	XX	—
(7) <i>lobicornis</i>	**	**	**	**	*	*	**	**	*	—	X
(8) <i>lundi lundi</i>	**	**	*	*	*	*	**	*	*	—	X
(9) <i>lundi pubescens</i>	**	**	**	*	**	*	**	**	*	X	XX
(10) <i>lundi parallelus</i>	**	**	**	*	**	*	**	*	*	X	—
(11) <i>rugosus rugosus</i>	**	*	**	**	**	*	*	*	*	XX	X
(12) <i>subterraneus subterraneus</i>	*	**	**	**	**	*	**	**	*	XXX	—
(2) Subgenus <i>Moellerius</i>											
(13) <i>beyeri</i>	**	**	*	**	*	*	**	**	*	—	XX
(14) <i>landolti balzani</i>	**	**	*	*	**	*	*	*	*	—	XX
(15) <i>landolti fracticornis</i>	**	**	*	**	**	*	*	*	*	—	XXXX
(16) <i>striatus</i>	**	**	**	*	**	*	**	**	*	XX	X
(2) Genus <i>Atta</i>											
(3) Subgenus <i>Palaeatt</i>											
(22) <i>saltensis</i>	**	**	**	*	**	*	**	**	**	XX	X
(4) Subgenus <i>Neoatta</i>											
(17) <i>capiguara</i>	**	**	*	**	**	*	**	**	**	XX	XXX
(18) <i>laevigata</i>	**	**	**	**	**	*	**	**	*	XXX	XXX
(19) <i>sexdens subropilosa</i>	*	**	**	**	**	*	**	**	**	XXXXX	—
(20) <i>sexdens priventris</i>	**	**	**	**	**	*	**	**	**	XX	X
(21) <i>volleneideri</i>	**	**	**	*	*	*	**	**	**	X	XXXX

*forest (1.0); **grass-land (2.0); ***both (1.5).

*fallen vegetation (1.0); **cut and carry (2.0); ***cut and drop (3.0).

*dicots (1.0); **grasses (2.0); ***both (1.5).

*Chaco (1.0); **Eastern Paraguay (2.0); ***both (3.0).

*superficial (1); **compact (2); ***dispersed (3).

*dumped on surface (1); **not dumped on surface (2).

*absent (1); **present (2).

*absent (1); **linear (2); ***circular (3).

*absent (1); **present transitional (2); ***present developed (3).

- 3—Large ants. Large nests with well developed trails *Atta* 4
- Medium sized ants. Small nests, at times medium to large. Trails smaller and not as wide, usually less than 20 m in length. *Acromyrmex* 7
- 4—Nest is a large mound, convex, and almost always covered with vegetation. Nest entrances open at ground level. No secondary mounds visible. Major workers with brilliant, huge head. Ants cut both grasses and dicots. *Atta laevigata*
- Nest consisting of loose soil, dispersed over several meters and concentrated to form several mounds, or with only one mound which is without a covering of vegetation 5
- 5—Small, convex mound, without a vegetative cover; often with terraces at 4 to 6 cm apart in sites protected from meteorological inclemencies. Trails originating often many meters from the mound. Head of the major worker red, more or less brilliant or somewhat dull, and rounded at the edges. Cutters of dicots *Atta saltensis*
- Mound of nest consisting of loose soil, and presenting several smaller secondary mounds. Main mound often with a slight cover of vegetation. Major workers without brilliant red heads 6
- 6—Nest consisting of a large mound, often with terraces if located in sites protected from the wind and rain, with many smaller secondary mounds located at various meters from the main mound. Nest entrances open near the secondary mounds, or open away from any external evidence of the nest. Head of the soldier dully brilliant, and smells of lime when crushed. Ants cut principally dicots *Atta sexdens*
- Nest similar, but with many secondary mounds and the main mound much reduced. Nest entrances open below ground level. Nests are almost always located in well lighted areas, and never under a vegetative canopy. Major workers rarely seen, and do not smell of lime when the head is crushed. Cutters of grasses principally but will cut dicots in quantity *Atta capiguara*
- 7—Nests superficial, covered with straw or dried vegetation. Ants a dark brown or black. Cutters of dicots. *Acromyrmex crassispinus* or *Acromyrmex coronatus*.
- Subterranean nests, often hard to find. Cutters of grasses and dicots 8
- 8—Nests marked by a superficial mound of loose soil, with entrances situated in small mounds which are often some distance from the main mound, or with a large mound, resembling a young nest of *Atta sexdens*. Ants light brown to dark brown. Cutters of dicots *Acromyrmex subterraneus* or *Acromyrmex rugosus*
- Nests resembling young nests of *Atta sexdens* 9
- 9—Nests characterized by small protruding mounds of loose soil 10
- Nests and entrances hard to find; without external evidence of their presence. Trails often excavated and thatched 11
- 10—Ants yellowish-brown. Cutters of dicots and grasses *Acromyrmex lobicornis*
- Ants dark brown to black. Cutters of dicots *Acromyrmex crassispinus*, *Acromyrmex hispidus*, *Acromyrmex disiger*, *Acromyrmex lundii*, or *Acromyrmex ambiguus*.
- 11—Ants black, or with a dark head and a darker gaster. Cutters of dicots *Acromyrmex lundii*
- Ants a dark metallic color, uniformly colored. Cutters of dicots *Acromyrmex laticeps*
- 12—Nests large with large major workers. Trails wide and long. *Atta* 13
- Ants small to medium. Trails thin, usually less than 20 m long or not present. *Acromyrmex* 16
- 13—Nests located in heavy clay soils. Mounds convex and without vegetative cover. Entrances on the mound surface in the form of raised tur-rents, 4 to 6 cm high, which orient outwards. Trails numerous and radiating from the mound in all directions. Major workers with red, wrinkled heads. Cutters of primarily grasses but will cut dicots *Atta vollenweideri*
- Nests located in red, sandy soils (*A. saltensis* will nest in clay soils.) 14
- 14—Nest mound convex and low, often with terraces 5 to 6 cm apart, free of a vegetative cover. Trails originate several meters from the main mound. Head of major worker rounded at the edges, dully brilliant. Cutters of dicots *Atta saltensis*
- Nests marked by loose soil, presenting various mounds, or of one large, convex mound covered with vegetation 15
- 15—Mound convex and tall, with a cover of vegetation. Entrances open at ground level. Secondary mounds absent. Major workers with a

bright red head, very much rounded at the edges. Cutters of dicots and grasses
Atta laevigata

—Nests marked by loose soil, present in several mounds, often with a covering of weeds. Soldiers rarely seen. Primarily cutters of grasses
Atta capiguara

16—Nests small to medium in size, presenting a mound of loose soil, often covered with vegetation. Detritus dumped to one side of the mound. Entrances present on the mound, and are thatched and elevated, in the form of turrets. Ants light to dark brown. Cutters of grasses *Acromyrmex landolti*

—Nests without external detritus heap or thatched turrets as entrances 17

17—Nests hard to find, similar to small nests of *Atta sexdens* or with several small mounds of loose soil from which entrances open 18

—Subterranean nests, characterized by only one mound of loose soil near the entrance. The entrance is neither elevated nor thatched. Ants dark brown to black. Cutters of dicots and grasses. *Acromyrmex lobicornis*, *Acromyrmex striatus*, *Acromyrmex beyeri*, *Acromyrmex disciger*, *Acromyrmex hispidus* or *Acromyrmex crassispinus*.

18—Nest with entrances located in various small mounds, or in one large mound, similar to a young nest of *Atta sexdens*. Ants a light to dark brown. Cutters of dicots. *Acromyrmex rugosus*.

—Subterranean nests, hard to find. Entrances without external markings of their presence. Trails often hidden under grass cover. Ants dark brown to black. Cutters of dicots. *Acromyrmex ambiguus*, *Acromyrmex striatus*, *Acromyrmex laticeps*, *Acromyrmex lundii*, *Acromyrmex beyeri* or *Acromyrmex crassispinus*

Canonical identification of Paraguayan leaf-cutting ants

The discriminating ability of the canonical correlation analysis was quite good (Fig. 1), with the majority of the species and subspecies separated along the canonical axis. The fit of the taxon (criteria) values with those of ethology and ecology (predictors) was extremely good ($r_1^2 = 0.817$, $X^2 = 36.969$, $P = 0.017$). For practical usage in the field for control purposes, this model will work quite suitably for determining what group the species in question falls into, and, consequently, how it should be controlled. For cases

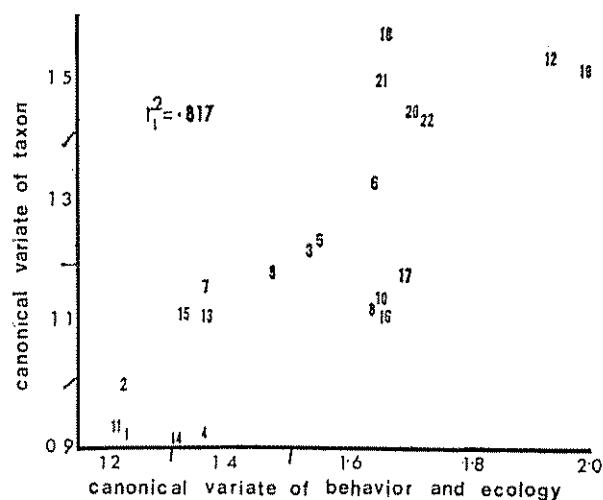


Fig. 1 The ubication of the Paraguayan species and subspecies of *Atta* and *Acromyrmex* along the canonical variates of taxon and behavior and ecology. Location of the species derived from the formula in Table 2. Numbers refer to the species numbers given in Table 1

in which the discrimination of species is not good (i.e., *Acromyrmex crassispinus* and *Acromyrmex hispidus fallax*, *Acromyrmex disciger* and *Acromyrmex rugosus*); a perusal of Table 1 will further facilitate identification if necessary. Also, the distribution of the species (2) will allow an almost certain identification in those cases where canonical variates may lead to the same variable loadings for both predictors and criteria.

The loadings of the canonical variates (Table 2) indicate that the foraging strategy of the species in question is the best indicator of the taxonomic rank of the species in question. Nest type also load in heavily. An identification to genus level is almost always possible. However, in the case of *Acromyrmex subterraneanus* it can be seen (Fig. 1), that this species is ranked at the same level as species of *Atta*, and may add credence to the common misnomer of local farmers in considering this a species of *Atta*.

Relative pest status of the Paraguayan leaf-cutting ants

Based upon our observations in the field and our conversations with local farmers, we have derived a rough scheme for the relative pest status of Paraguayan *Atta* and *Acromyrmex*. These data are derived in part from the general distribution (2) and biology (2) of the species in question. It should be pointed out that leaf-cutters can produce extremely deleterious localized damage, and are not damaging to the country as a whole. Although it is extremely difficult to derive an estimate of the economic losses incurred by farmers due to the activities of these ants, our observations would indicate that *Atta sexdens*, *Atta laevigata*

Table 2 Canonical loadings of behavioral and ecological characteristics (predictor vector) and taxon and size characteristics (criteria vector).

Variable	Part 1: Canonical vector normalized to give unit within-group sum square & sum cross product (weighting values)	Part 2: Canonical vector standardized to have unit total variance and scaled to have maximum weighting of unity
Criteria:		
Genus	-0.2276	-1.0000
Subgenus	-0.0103	-0.0151
Worker size	0.2109	0.9266
Predictors		
Foraging strategy	0.3091	1.0000
Foraging territory	0.1432	0.4632
Foraging trails	0.1144	0.3701
Detritus disposal	-0.0726	-0.2349
Nest type	0.2848	0.9214
Galleries	0.1220	-0.3950
Habitat	-0.0023	-0.0074

and *Acromyrmex subterraneus* are the principal pests of orchards and broad leaf dicots for the country as a whole (Table 1), while the major species affecting the cattle industry through the removal of suitable forage are *Atta vollenweideri*, *Atta laevigata*, *Atta capiguara*, and *Acromyrmex landolti*. The remaining species can, however, cause considerable localized damage to crops or pasturelands under the proper conditions.

Conclusions

Based on a comparison of a traditional field key and canonical comparison of the species in question, a more reasonable identification of Paraguayan leaf-cutting ants can be achieved through the latter. The use of the discriminating ability of this analysis involves a minimal amount of calculation, and can be readily carried out by field extension agents or local farmers themselves. Although the use of nominal values in canonical correlation analysis is sometimes misleading (7), in this case canonical analysis allows a more clear cut identification than a traditional field key.

Although it is difficult to assess the direct economic importance of the various species and subspecies, it would appear that species of *Atta* are more damaging at a national level than *Acromyrmex*. As further studies focus on the economics of these species, this relationship will be further clarified. Nevertheless, we feel that there will be little change in our relative pest ranking.

Summary

Leaf-cutting ants of the genera *Atta* and *Acromyrmex* are considered the major polyphagous pests of Paraguayan agricultural and ranching operations. Based on a previous survey of these genera, 22 species and subspecies are known to occur in Paraguay. As species exhibit characteristic behaviors and ecologies, a suitable method of control for one species may not be applicable for others. Due to this fact, and to the fact that an accurate taxonomic identification is not readily obtained by extension agents and untrained taxonomists, a simple multivariate formula was derived based upon dichotomous species characteristics of biology. This canonical analysis allows the discrimination of species readily in the field, with minimal calculations. This means of field identification is compared with a traditional field key, based upon the same information. The relative pest status of the known species and subspecies of *Atta* and *Acromyrmex* is also given.

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Notas y Comentarios

Conservación de germoplasma de tomate

El tomate es un caso clásico de una planta que ha sido mejorada considerablemente por hibridación con cultivares primitivos y especies silvestres afines. En los últimos 40 años se han transferido genes de resistencia a la fusariosis, al Verticillium y a los nematodos. Actualmente se trata de transferir alto contenido de sólidos en el fruto y resistencia a otras enfermedades.

Pero, por otro lado, los cultivares importados y los nativos mejorados han reemplazado completamente a los tipos primitivos en la costa del Perú, en donde proceden posiblemente ocho de las nueve especies existentes de *Lycopersicon*. Al extinguirse los cultivares primitivos, gente como Charles M. Rick de la Universidad de California, en Davis, señalan la importancia de las colecciones de germoplasma (*Agricultura de las Américas*, noviembre 1978, p. 17). La más importante es la de Davis y desde 1948, en que se inició la primera expedición a las zonas de origen, se ha utilizado el material recolectado en el mejoramiento del tomate.

La tolerancia a la salinidad de *L. chesmani*, detectada en su hábitat de las islas Galápagos, es un caso interesante. Las observaciones hechas demostraron que las plantas toleraban, aunque con crecimiento reducido, hasta 100 por ciento de agua de mar en sus raíces, y que esa capacidad de sobrevivir esos niveles de salinidad se basaba en la resistencia de los tejidos de la planta y no a una barrera que impedía la absorción de la sal. (Cf. *Turrialba* vol. 28, p. 360).

Por su parte, *Solanum pennellii*, que se puede cruzar fácilmente con el tomate, crece sólo en lugares muy secos de las quebradas del oeste peruano. Virtualmente no recibe más precipitación que la condensación de las neblinas frecuentes en la zona. Tiene, pues, una resistencia natural a la sequía.

El alto contenido de sólidos solubles en el fruto se descubrió al sembrar *L. chmielewskii* y se determinó que aunque es más del doble que el de las especies cultivadas, es totalmente inservible en esos frutos pequeños, del mal sabor y de maduración verde. Pero cruzando esa especie con un cultivar corriente, retrocruzando cinco generaciones y finalmente sometiendo el material a la selección, se produjeron tomates grandes de maduración roja con 50 por ciento más de contenido de sólidos.

Otros desarrollos han seguido a los estudios de este material genético. La variabilidad del germoplasma se puede medir ahora por métodos bioquímicos. Por ejemplo, la separación e identificación de isozimas permiten una determinación simple y mucho más precisa de la variabilidad genética. Con este método se determinó que la autopolinización predomina en las especies *L. chesmanii* y *L. parviflorum*, en tanto que los

sistemas de cruzamiento son muy diferentes en *L. pimpinellifolium* de un lugar a otro. Las pruebas han indicado que todas las especies silvestres se pueden hibridar con los cultivares de *L. esculentum*. Por otro lado, hay especies como *L. chilense* y *L. peruvianum* que no pueden autopolinizarse y dependen de la polinización cruzada.

Todo esto indica la importancia del mantenimiento de las colecciones de germoplasma de los principales cultivos del planeta. Si se tiene en cuenta que ciertas poblaciones de *L. hirsutum* y *L. peruvianum*, conocidas hace 25 años, ya no existen, es bueno saber que en ciertas colecciones existen ejemplares vivos cuya supervivencia está asegurada.

Sol y arena, fijadores del nitrógeno

La arena del desierto cataliza la conversión del nitrógeno atmosférico a amoníaco bajo el impacto de la luz solar. El Dr. Gerhard Schrauzer, de la Universidad de California, en San Diego, manifestó en una reunión reciente de la American Chemical Society, en Savannah, Georgia, que sus resultados sugieren que una hectárea de desierto arenoso podría producir 2 a 20 kilogramos de amoníaco al año. Los 2,7 millones de hectáreas de este tipo de desierto de todo el mundo podrían por consiguiente rendir de 7,5 a 75 millones de toneladas de amoníaco anualmente. Estos nuevos resultados pueden dar lugar a una revisión drástica de los estimados de las fuentes y del equilibrio del amoníaco en la atmósfera. El amoníaco artificial claramente representa una proporción mucho más pequeña de lo que se había pensado, representando la fijación, por microbios y ahora, según parece, por la arena, un papel importante (*New Scientist* 8 febrero 1978, p. 383).

Schrauzer cree que esta reacción fotoquímica es importante para la producción de amoníaco en Marte y en otros planetas y sugiere que un día la reacción puede quizás ser empleada industrialmente en regiones áridas. Encuentra que una fracción de uno por ciento de arena natural rica en dióxido de titanio y de hierro es responsable por 60 a 80 por ciento de la actividad fijadora del nitrógeno. Esto parece ser un equivalente natural directo del dióxido de titanio con impurezas de hierro que actúa como catalizador de reacciones fotoquímicas similares en el laboratorio. Una célula solar que utiliza este catalizador y que produce 120 a 250 kilogramos de amoníaco por hectárea y por año ha sido ya construida, pero el rendimiento es demasiado bajo para uso industrial práctico. Los procesos futuros probablemente podrían involucrar el uso de camas de catalizador alimentadas con aire húmedo tibio y luz del sol concentrada con espejos. El amoníaco producido podría ser absorbido *in situ* por ácido fosfórico para rendir fertilizantes a base de fosfato de amonio.