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SMALL MAMMALS IN AGRICULTURAL AREAS OF THE WESTERN LLANOS OF VENEZUELA: COMMUNITY STRUCTURE, HABITAT ASSOCIATIONS, AND RELATIVE DENSITIES

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We used mark–recapture and removal trapping during 37 months to examine structure of small-mammal assemblages in agricultural and pastoral areas on the western llanos of Venezuela. Among 34 sites sampled, species richness, diversity, population densities, and relative contribution to the assemblage by 10 rodent and 3 marsupial species varied by habitat or land-use category, major vegetative formation, and (within agricultural systems) crop species. Most habitat types, especially relatively uniform areas of mechanized agriculture, were numerically dominated by 2 rodents, *Sigmodon alstoni* and *Zygodontomys brevicauda.* Subsistence agriculture plots were more variable and had the highest species richness and diversity. Peridomestic habitats were dominated by *Rattus rattus.* In contrast to findings in agroecosystems in the United States and Argentina, relative densities were not lower in crop fields than in adjacent borders nor were there differences in the structure of the rodent assemblages. Captures of *Heteromys anomalus, Oecomys speciosus,* and *Oecomys trinitatus* document range extensions for these species on the western llanos.

Key words: community structure, habitat associations, llanos, *Oligoryzomys fulvescens, Rattus rattus, Sigmodon alstoni,* Venezuela, *Zygodontomys brevicauda*

Structure of small-mammal assemblages in nonforest areas of the Venezuelan llanos has been described by O'Connell (1981), August (1983), Vivas and Calero (1985), and Soriano and Clulow (1988). These authors conducted studies in relatively undisturbed areas of primarily native vegetation, and most previous studies have been restricted to a small area of the central llanos. Very little is known about small-mammal assemblages in the ecologically distinct western llanos. Furthermore, as with other grassland habitats throughout the world, a large proportion of the llanos has been adapted for human use. Some land-use categories, such as ranching, may result in relatively minor changes to the environment. Others, such as agriculture, result in more profound changes. The extreme habitat modifications resulting from agricultural development also may result in substantial changes in the small-mammal assemblage that occupies the area. Structure of small-mammal populations in agricultural areas of the llanos has never been described.

There are practical reasons for understanding the structure and dynamics of rodent populations in agricultural and peri-

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domestic habitats of the llanos. Although the impact of rodents as crop pests on the llanos has never been specifically quantified, the most dominant genera on the western llanos (including *Zygodontomys, Sigmodon,* and *Oryzomys*) are associated with frequent damage to crops in Latin America (Elias and Fall 1988). In addition, medical scientists have recently become aware of the transmission of several serious pathogens from wild rodents to humans in rural environments. In South America, these pathogens include arenaviruses and hantaviruses that cause South American hemorrhagic fevers and hantavirus pulmonary syndrome, respectively (Childs et al. 1995; Ellis et al. 1995). *Z. brevicauda* is the reservoir for Guanarito arenavirus, etiologic agent of Venezuelan hemorrhagic fever (de Manzione et al. 1998; Tesh et al. 1993). Other rodent species occurring on the llanos that are associated with hantaviruses and arenaviruses include *S. alstoni* (Fulhorst et al. 1997a, 1997b), *S. hispidus* (Glass et al. 1998), and *Oligoryzomys fulvescens* (C. F. Fulhorst, pers. comm.). Because most rodent–human contact (thus most virus transmission) occurs in agricultural or peridomestic settings, an understanding of the structure and dynamics of rodent assemblages in these areas has public health importance.

Here, we describe the general structure of rodent assemblages of the western llanos of Venezuela with emphasis on agroecosystems. We evaluated differences in the structure of rodent assemblages among major biotic formations, various land-use categories, and specific agricultural systems and compared our findings with results from previous studies of small mammals in natural habitats.

Materials and Methods

Study area.—The Venezuelan llanos are an inland plain covering about 240,000 km^2 bounded by the Andes and the Venezuelan coastal range to the west and north and the Orinoco River to the south and east. Our study was confined largely to that geographic subunit referred to as the western llanos in the states of Portuguesa, Barinas, Apure, Cojedes, and western Guárico (Fig. 1). Elevations in the study area ranged from 300 m in the foothills of the Andes (northwest) to about 50 m in the south and east. About 80% of the surface area was covered by savanna; the remainder included deciduous, semideciduous, and gallery forests. The western llanos has pronounced rainy and dry seasons; 1,000–2,000 mm of annual rain falls mostly in May–November (Ramia 1967; Sarmiento and Monasterio 1969). There was a cline of increasing rainfall and decreasing temperature from east to west across the study area. Precipitation increased from about 1,000 mm/year in western Guárico State to about 1,800 mm/year in northwestern Barinas. Mean annual, mean maximum, and mean minimum temperatures, respectively, were 27°C, 33°C, and 22°C in western Guárico and 23°C, 31°C, and 21°C in northwestern Barinas (Venezuelan Air Force, in litt.).

Trapping sites were in the 4 primary natural vegetation types represented in the study area. Piedmont was the area of ≤300 m elevation at the base of the Andes in northern Portuguesa and Cojedes. It included piedmont savanna and semideciduous tropical forest (Sarmiento 1983). Below the Piedmont, there were 3 natural savanna formations (Ramia 1967). The savannas of banco, bajío, and estero (literally bank, lowland, and marsh; referred to hereinafter as lowland savanna) were restricted largely to the western llanos and southern part of the central llanos. The elevated bancos supported gallery forest or a treeless savanna of grasses. The bajíos were covered by ≤20 cm of water during the rainy season and supported a high diversity of annual and perennial grasses and sedges. During the rainy season, the esteros were transformed into shallow lakes ≥1 m deep with abundant aquatic vegetation. During the dry season, the esteros were covered by a relatively species-poor community of low grasses and sedges (Ramia 1967; Sarmiento 1983).

Paspalum savanna occurred on the flood plains of rivers and streams in the lowest parts of the llanos in southern Cojedes and Portuguesa, southeastern Barinas, and northeastern Apure. They supported a luxurious growth of *P. fasciculatum,* a bunch grass that reached 2.5 m in height during the dry season but was inundated during the wet season. In the western llanos,

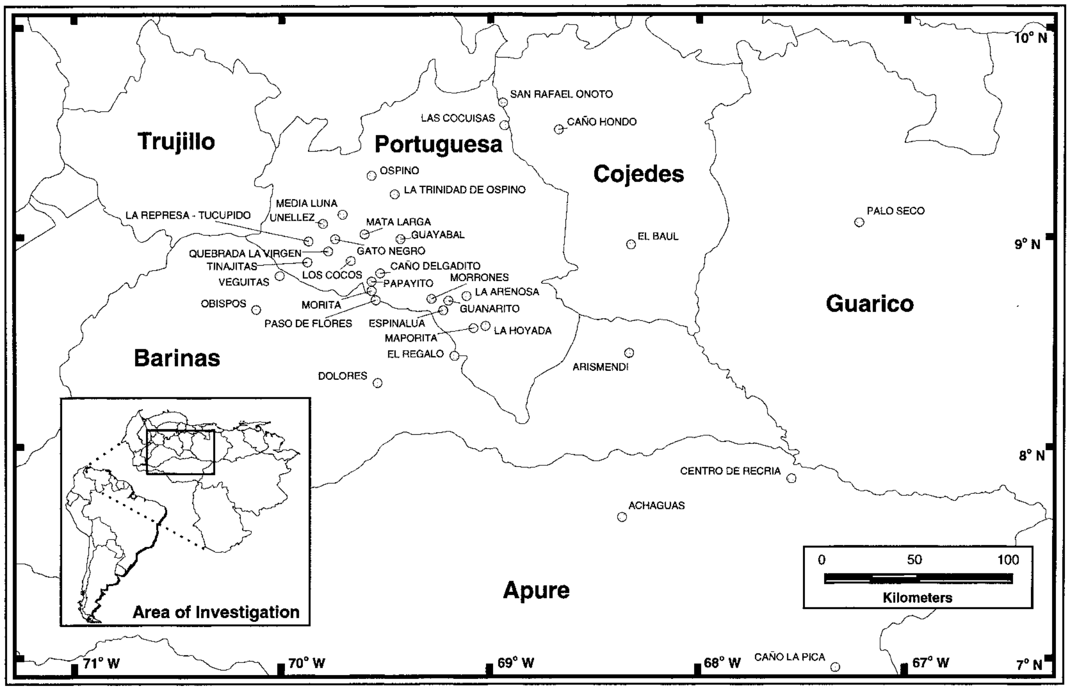

FIG. 1.—The 34 sites where small mammals were sampled on the western llanos of Venezuela, January 1994–January 1997.

Trachypogon savanna occurred primarily in southern Apure State with a few isolated patches in the northern Piedmont. They had well-drained sandy soils and supported 5 species of bunch grass (*Trachypogon*) reaching 0.5–1 m in height.

A large part of the western llanos has been altered by agriculture and cattle ranching. The majority of our trapping sites, although included within 1 of 4 vegetation types, were in areas associated with those activities. Principal crops subjected to mechanized agriculture were corn, sorghum, and sugar cane. Corn and sorghum were planted in the early rainy season (April–June) and harvested in August–October. Fields were fallow the rest of the year. Sugar cane was harvested during the dry months (January–April). Individual fields were harvested progressively in small patches that are immediately replanted, so that little land was fallow at any time.

Specific habitats in which we trapped included the crops listed above and the following: subsistence agriculture plots of generally <3 ha with corn, beans, manioc, peppers, orange, papaya, plantain, guava, and passion fruit; pasture often planted with *Cynodon nlemfuensis*; and borders of relatively undisturbed linear habitats adjacent to crop fields and pastures characterized by high coverage of grasses and forbs. Peridomestic habitats included the immediate vicinity of homes on farms or in small villages. Roadsides had a stable, high cover of herbaceous vegetation but, unlike borders, were not associated with any crop.

Small-mammal sampling.—During January 1994–January 1997, trapping teams visited 34 sites on the western llanos (Fig. 1). During each visit, about 600 Sherman live-capture traps (7.5 by 9 by 23 cm) were set each night for 3 consecutive nights. Traps, baited with chunks of pineapple, were placed 10 m apart in agricultural fields and their borders, roadsides, pasture, and peridomestic areas. In peridomestic habitats, Sherman traps were supplemented with approximately 40 Tomahawk live-capture traps (14 by 14 by 40 cm).

Sampling in the various vegetative formations occurred as follows: lowland savanna—monthly, January 1994–December 1996; *Paspalum* savanna—March, April, June, and November 1994, February and April 1995, January and March 1996; *Trachypogon* savanna—March

1995 and February 1996; piedmont savanna—April, June–August 1994, January and May 1995, April and May 1996, January 1997.

Each morning, captured animals were taken to an isolated outdoor site where they were euthanized using chloroform and then necropsied. For each animal captured, we recorded date, habitat, locality, gender, reproductive condition, weight, total length, and lengths of tail, head plus body, ear, and hind foot. Species identifications were confirmed at the Museum of Natural Sciences of Guanare, National Experimental University of the Western Llanos, Guanare, Portuguesa State, Venezuela. Alcohol-preserved samples of each species (about 15% of total captures) are archived at the Museum of Natural Sciences of Guanare. A smaller sample (57 animals) is archived at the American Museum of Natural History, New York.

Standard methods were used to minimize risk of infection with rodent-borne pathogens (Mills et al. 1995a, 1995b). We wore latex gloves and respirators fitted with high-efficiency particulate air filters and decontaminated instruments and working surfaces with 10% bleach after necropsies. Carcasses not preserved in formalin were burned at the site.

Data analysis.—Direct counts of trapped species (*N0*—sensu Ludwig and Reynolds 1988) were used to measure species richness. Because sample sizes varied greatly among sampling units, we used rarefraction (Ludwig and Reynolds 1988), a technique that adjusted for differences in number of individuals sampled to allow comparisons of richness among vegetative formations and habitats. Diversity indices (*N1* and *N2*—Hill 1973) were used to measure numbers of abundant and very abundant species, respectively (Ludwig and Reynolds 1988). Evenness was measured using the modified Hill's (1973) ratio (*E5*). Differences in the structure of rodent assemblages among vegetative formations and habitats were evaluated by comparing capture frequencies of the major species with a chi-square test (Zar 1974). Rare species (<5% of total captures) were eliminated from comparisons to avoid violation of assumptions (concerning minimum expected numbers) of chi-square analysis. *S. alstoni*, *Z. brevicauda*, *O. fulvescens*, and *R. rattus* were included in comparisons among formations. *R. rattus* was excluded from further comparisons among habitats (within lowland savanna) to meet assumptions of the analysis. Peridomestic habitat was excluded from comparisons because the trapping protocol differed in that habitat (Sherman traps supplemented with Tomahawk traps).

For the most frequently captured species (*S. alstoni*, *Z. brevicauda*, and *O. fulvescens*) differential use of habitats or land-use categories by subpopulations (males versus females and sexually mature versus immature individuals) was analyzed using chi-square analysis (Zar 1974). Observed frequencies in each habitat or land-use category were compared with expected frequencies of each gender or reproductive category based on their overall proportions in the sampled population. Mature males were those with scrotal testes; mature females were either pregnant or lactating or had open vaginas. Significance level for individual chi-square tests was adjusted to $\alpha = 0.0008$ for an experiment-wise error rate of 0.05.

RESULTS

Small-mammal assemblage.—From January 1994 through January 1997, 2,508 individual mammals were captured during 34,455 trap nights, for a success rate of 7%. The assemblage represented by our sampling consisted of 13 species, including 10 rodents and 3 marsupials (Table 1). Although some species were common throughout the study area, many were rare and local. *S. alstoni* was the most frequently captured species, accounting for 48% (n = 1,196) of captures, and *Z. brevicauda* was second (37%; n = 925). *R. rattus* and *O. fulvescens* comprised about 5% of captures each, *S. hispidus* accounted for about 2%, and 8 other species contributed <1% each.

Distributions of the small mammals captured during our study included extensions of previously known ranges for several species rarely or never before captured on the western llanos. *Heteromys anomalus* has been captured on the central llanos (Masaguaral, Guárico State—Eisenberg et al. 1979; Linares 1998) but has never been reported from the western llanos. We captured *H. anomalus* at Caño Hondo and El Baul (Cojedes, Fig. 1), Dolores, El Regalo, and Veguitas (Barinas), and La Represa-

TABLE 1.—Numbers of small mammals captured, trapping effort, trap success, richness (count of number of species), adjusted richness by rarefraction, diversity, and evenness of assemblage in various vegetative formations on the llanos of Venezuela, January 1994–January 1997 (lowland savanna = banco, bajío, and estero; *Paspalum* = *Paspalum fasciculatum* savanna; Piedmont = piedmont savanna; *Trachypogon* = *Trachypogon* savanna).

Measure	Lowland	*Paspalum*	Piedmont	*Trachypogon*	Total
Species (*n* [%])					
Didelphimorphia					
Didelphis marsupialis	6 (0.4)	2 (0.3)	0	0	8 (0.3)
Marmosa robinsoni	2 (0.1)	5 (0.8)	0	0	7 (0.3)
Monodelphis brevicaudata	2 (0.1)	0	2 (1.1)	0	4 (0.2)
Rodentia					
Heteromyidae					
Heteromys anomalus	7 (0.4)	2 (0.3)	6 (3.3)	0	15 (0.6)
Muridae					
Rattus rattus	43 (2.6)	104 (17.3)	6 (3.3)	0	153 (6.1)
Holochilus sciureus	4 (0.2)	8 (1.3)	0	0	12 (0.5)
Oecomys speciosus	2 (0.1)	0	0	0	2 (0.1)
Oecomys trinitatis	2 (0.1)	0	0	0	2 (0.1)
Oligoryzomys fulvescens	58 (3.5)	59 (9.8)	0	0	117 (4.7)
Sigmodon alstoni	910 (55.3)	154 (25.6)	74 (40.7)	58 (74.4)	1,196 (47.7)
Sigmodon hispidus	1 (0.1)	0	41 (22.5)	2 (2.6)	44 (1.8)
Zygodontomys brevicauda	600 (36.4)	262 (43.6)	45 (24.7)	18 (23.1)	925 (36.9)
Echimyidae					
Proechimys guairae	10 (0.6)	5 (0.8)	8 (4.4)	0	23 (0.9)
Total captures (*n*)	1,647	601	182	78	2,508
Trap nights (*n*)	23,762	3,692	4,556	2,445	34,455
Trap success (%)	6.9	16.3	4	3.2	7.3
Richness	13	9	7	3	13
Adjusted richness (n = 78)	6	6	7	3	7
Diversity (*N1*)	2.8	4.1	4.3	1.9	3.5
Diversity (*N2*)	2.3	3.4	3.6	1.7	2.7
Evenness (*E5*)	0.70	0.76	0.79	0.72	0.67
Number of sites	31	9	8	2	50
Number of visits	60	12	10	2	84

Tucupido and Quebrada la Virgen (Portuguesa). There is 1 record of *Oecomys trinitatus* from the western llanos (Barinas State—Linares 1998). We captured *O. trinitatus* at Gato Negro, Portuguesa State. There are only 2 records of *Oecomys speciosus* from the western llanos (southeastern Apure and Guarico states—Linares 1998). We captured *O. speciosus* at Dolores (Barinas) and La Trinidad de Ospino (Portuguesa).

Differences among natural formations.—Characteristics of the rodent assemblages varied among the 4 natural vegetative formations sampled (Table 1). Trap success was higher in *Paspalum* savanna (16%) than in any other vegetative type (3–7%). Trap success also was higher in lowland savanna (7%) than in *Trachypogon* or piedmont savanna (3–4%). Species richness was highest in lowland and *Paspalum* savanna (13 and 9 species, respectively) and lowest in *Trachypogon* savanna. Adjustment of richness values by rarefraction indicated that most observed differences in species richness may be due to differences in sample size, except for *Trachypogon* savanna where only 3 species were captured. The highest diversity indices were in *Paspalum* and piedmont savanna, and the lowest was in *Trachypogon* savanna. The relatively low diversity in lowland savanna probably was derived from low evenness: >90% of captures comprised only 2 species (*S. alstoni* and *Z. brevicauda*).

Sigmodon alstoni comprised >40% of captures in all vegetative types except *Paspalum* savanna (26%). *Z. brevicauda* was captured in all vegetative types, with the highest representation in *Paspalum* savanna (44%), nearly twice that in *Trachypogon* savanna and piedmont savanna. *Proechimys guairae* comprised ≤4% of captures in all vegetative types. *S. hispidus* was captured almost exclusively in piedmont savanna, where it represented 23% of captures. *R. rattus* was an important member of the assemblage only in *Paspalum* savanna (17% of captures). *O. fulvescens,* which comprised 10% of captures in *Paspalum* savanna, was captured only in that vegetative type and lowland savanna.

There were significant differences in structure of the small-mammal assemblage among vegetative types, comparing relative frequencies of captures of the dominant rodent species (*S. alstoni, Z. brevicauda, O. fulvescens,* and *R. rattus*). All pairwise comparisons among vegetative types differed ($P < 0.01$), except for piedmont savanna versus lowland savanna ($\chi^2 = 6.6$, $P = 0.08$).

Habitat associations.—To limit potential confounding by differences among vegetative formations, geographic locations, and season of sampling, comparisons of small-mammal assemblages among habitats were restricted to lowland savanna, the most frequently sampled natural formation. Lowland savanna, which is restricted to southern and central Barinas and Portuguesa, northern Apure, and southwestern Guárico states, accounted for 69% of trap nights and 69% of captures (23,762 trap nights, 1,647 captures).

The characteristics of the small-mammal assemblage varied among the 5 major habitat types within lowland savanna (Table 2). Relative density of small mammals, as indicated by trap success, was highest in areas of mechanized agriculture and lowest along roadsides. Subsistence agriculture had the highest richness and diversity, followed by roadside. Mechanized agriculture and pasture had the lowest adjusted richness, and although peridomestic habitat had a slightly higher adjusted richness than mechanized agriculture or pasture, the domination of that habitat by *R. rattus* resulted in very low evenness.

There were significant differences in the structure of the rodent assemblages (based on the proportional distributions of *S. alstoni*, *Z. brevicauda*, and *O. fulvescens*) among all pairwise comparisons of habitats ($P < 0.02$), except for subsistence agriculture versus all other habitats ($P > 0.07$). Structure of rodent assemblages in mechanized

TABLE 2.—Numbers of small mammals captured, trapping effort, trap success, richness (count of number of species), adjusted richness by rarefaction, diversity, and evenness of assemblage on the llanos of Venezuela, January 1994–January 1997 in various habitats and land-use areas within lowland savanna.

Measure	Mechanized agriculture	Pasture	Peridomestic	Roadside	Subsistence agriculture	Total
Species (n [%])						
Didelphimorphia						
Didelphis marsupialis	3 (0.3)	0	0	3 (1.2)	0	6 (0.4)
Monodelphis brevicaudata	1 (0.1)	0	0	0	1 (2.2)	2 (0.1)
Marmosa robinsoni	0	0	0	2 (0.8)	0	2 (0.1)
Rodentia						
Heteromyidae						
Heteromys anomalus	1 (0.1)	0	0	1 (0.4)	5 (11.1)	7 (0.4)
Muridae						
			42			
Rattus rattus	0	0	0 (80.8)	1 (0.4)	0	43 (2.6)
Holochilus sciureus	3 (0.3)	1	0	0	0	4 (0.2)
Oecomys speciosus	0	0 (0.2)	0	2 (0.8)	0	2 (0.1)
Oecomys trinitatis	0	0	0	2 (0.8)	0	2 (0.1)
Oligoryzomys fulvescens	32 (3.7)	13	0	10 (4.1)	3 (6.7)	58 (3.5)
Sigmodon alstoni	502 (57.8)	276 (3.1)	3 (5.8)	103 (42.4)	23 (51.1)	907 (55.8)
Sigmodon hispidus	1 (0.1)	0 (66)	0	0	0	1 (0.1)
Zygodontomys brevicauda	323 (37.2)	126 (30.1)	6 (11.5)	118 (48.6)	12 (26.7)	585 (36.0)
Echimyidae						
Proechimys guairae	2 (0.2)	2 (0.5)	1 (1.9)	1 (0.4)	1 (2.2)	7 (0.4)
Total captures (n)	868	418	52	243	45	1,626
Trap nights (n)	10,357	5,979	730	5,380	766	23,212
Trap success (%)	8.4	7	7.1	4.5	5.9	7
Richness	9	5	4	10	6	13
Adjusted richness (n = 45)	3	3	4	5	6	
Diversity (*N1*)	2.4	2.1	1.9	3	3.6	2.9
Diversity (*N2*)	2.1	1.9	1.5	2.4	3	2.3
Evenness (*E5*)	0.78	0.76	0.54	0.72	0.75	0.68
Number of sites	24	7	10	17	5	31
Number of visits	36	24	13	21	5	60

agriculture and pasture was similar; about two-thirds of the captures were *S. alstoni*, one-third was *Z. brevicauda*, and a small proportion (<4%) was *O. fulvescens*. The assemblage in subsistence agriculture was dominated less by *S. alstoni* and had a higher representation of *O. fulvescens* (7%), and there was a relatively large component (11%) of *H. anomalus*. Failure to find statistical differences in the structure of subsistence agriculture compared with other habitats likely was related to the small sampling effort and consequently small samples in that habitat. The assemblage in roadside habitats differed from those in mechanized agriculture and pasture in that the proportion of *Z. brevicauda* (49%) exceeded that of *S. alstoni* (42%). Peridomestic habitat was dominated by *R. rattus* (81%) and *Z. brevicauda* (12%).

Characteristics of the small-mammal assemblage also varied among the major mechanized crop systems (Table 3). Species composition and trap success varied relatively little between crops and adjacent borders. Higher species diversity and richness were observed in border habitats of sugar cane and sorghum than in corresponding cultivars. In contrast, diversity and richness was comparable in corn fields and adjacent borders. The small-mammal assemblage in sugar cane was dominated by *Z. brevicauda*; sorghum was almost completely dominated by *S. alstoni*; corn was fairly evenly divided between the 2 species. Trap success was highest in corn and lowest in sugar cane. There were no differences in use of habitats or land-use categories between subpopulations (male versus female or sexually mature versus immature) for *S. alstoni*, *Z. brevicauda*, or *O. fulvescens*.

Discussion

Comparisons among principal vegetative types.—Small-mammal assemblages in agricultural and pastoral areas of the western llanos of Venezuela showed variations among natural formations, among habitat types or land-use categories, and among specific agricultural systems. Several factors may contribute to the uniqueness of *Paspalum* savanna among the types studied. Primary production in *Paspalum* savanna has been measured at 10–25 metric tons/ha compared with 4–9 tons/ha in lowland savanna and only 2–7 tons/ha in *Trachypogon* savanna (Medina 1980). This difference in primary productivity may translate into a higher carrying capacity for the community of consumers, including rodents. The decreased numerical dominance by *S. alstoni* and the increased importance of *O. fulvescens* in *Paspalum* savanna may be due to the relative adaptability of these species to habitats that are inundated during the wet season. *S. alstoni* has been described as a strictly terrestrial species that avoids water (Voss 1992). As a climbing species, *O. fulvescens* is well suited to survive periodic inundations (August 1984). The higher densities of *R. rattus* in peridomestic areas of *Paspalum* savanna may be due, at least in part, to regional variations in the efficacy of abatement programs conducted by the Ministry of Health in rural areas of Venezuela.

Comparisons among habitats.—Despite the relatively low trapping effort, subsistence agriculture had the highest adjusted species richness and highest diversity. It also had the highest representation of *O. fulvescens* and was the only habitat in which *H. anomalus* was an important member of the assemblage. This pattern is likely due to the relatively high vegetative diversity in subsistence agriculture and availability of high-energy food items.

Oligoryzomys fulvescens prefers multistratal tropical evergreen forests (Eisenberg 1989). A congener that also inhabits the llanos, *O. bicolor*, was captured frequently in trees (August 1984), implying scansorial habits. Subsistence agriculture was the only habitat sampled that would provide appropriate habitat for climbing species.

Although *H. anomalus* has not been reported as frequenting anthropogenic habitats, it inhabits multistratal tropical forests and gallery forests in association with

TABLE 3.—Numbers of small mammals captured, trapping effort, trap success, richness (count of number of species), diversity, and evenness of assemblage among crops and bordering habitats within lowland savanna on the llanos of Venezuela, January 1994–January 1997.

Measure	Sugar cane	Border	Corn
Species (*n* [%])			
Didelphimorphia			
Didelphis marsupialis	0	1 (1.4)	2 (1.6)
Rodentia			
Heteromyidae			
Heteromys anomalus	0	0	0
Muridae			
Holochilus sciureus	0	0	0
Oligoryzomys fulvescens	0	3 (4.2)	3 (2.4)
Sigmodon alstoni	0	10 (13.9)	65 (51.2)
Sigmodon hispidus	0	0	0
Zygodontomys brevicauda	4 (100)	57 (79.2)	57 (44.9)
Echimyidae			
Proechimys guairae	0	1 (1.4)	0
Total captures (*n*)	4	72	127
Trap nights (*n*)	90	1,249	1,061
Trap success (%)	4.4	5.8	12
Richness	1	5	4
Diversity (*N1*)	1	2	2.3
Diversity (*N2*)	1	1.5	2.2
Evenness (*E5*)		0.54	0.87
Number of sites	1	5	6
Number of visits	1	5	7

streams or rivers, where it feeds on seeds and fruits (Eisenberg 1989). Areas dedicated to subsistence agriculture on the llanos are frequently close to water sources and offer a wide variety of fruits and seeds. Cheek pouches of *H. anomalus* frequently contained seeds of crop species cultivated at the capture site.

Roadside habitat also had a relatively high species richness and was the only habitat (except for peridomestic) in which *Z. brevicauda* was captured more frequently than *S. alstoni*. *Z. brevicauda* is a habitat specialist that prefers dense herbaceous cover and sparse arborescent vegetation (August 1984). This description fits the roadside habitats we sampled. Similarly, Voss (1991) described *Z. brevicauda* as an opportunistic species that colonizes disturbed anthropogenic habitats with dense invasive vegetation. Our data support these observations.

There were not large differences in trap success between mechanized crop areas and their borders (Table 3), but trap success within fields of corn was slightly higher than in corresponding borders. This pattern is in contrast to that found in other agroecosystems, where uncultivated borders had higher small-mammal densities, species diversity, and richness in North America (Fleharty and Navo 1983; Mellink 1991) and South America (Ellis et al. 1997; Mills et al. 1991). On the pampa of Argentina, trap success in borders was about twice that in corn fields (Mills et al. 1991). This difference might be due, in part, to the fact that most rodent species in pampa agroecosystems are border habitat specialists rarely encountered in crop fields (Ellis et al. 1997;

TABLE 3.—Extended.

Border corn	Sorghum	Border sorghum	Total crop	Total border
0	0	0	2 (1.4)	1 (0.2)
0	0	1 (0.6)	0	1 (0.2)
3 (1.1)	0	0	0	3 (0.6)
14 (5.3)	0	8 (5.2)	3 (2)	25 (5.1)
140 (52.6)	16 (100)	119 (76.8)	81 (55.1)	269 (54.6)
0	0	1 (0.6)	0	1 (0.2)
108 (40.6)	0	26 (16.8)	61 (41.5)	191 (38.7)
1 (0.4)	0	0	0	2 (0.4)
266	16	155	147	493
3,371	255	1,756	1,406	6,376
7.9	6.3	8.8	10.5	7.7
5	1	5	4	8
2.4	1	1.6	2.3	2.6
2.3	1	1.6	2.1	2.2
0.93		0.95	0.86	0.79
10	3	5	8	16
10	4	6	11	19

Mills et al. 1992). In contrast, composition of rodent assemblages in corn fields and their borders in the western llanos were nearly identical: 51–53% *S. alstoni* and 41–45% *Z. brevicauda* (other species were rare). Differences in agricultural practices between the 2 areas also may be a factor. Corn fields in Argentina are treated with herbicides, and weedy vegetative cover is generally low. We did not measure cover by weeds in corn fields in Venezuela. However, for economic reasons, farmers on the llanos are less likely to invest in herbicides. The low small-mammal diversity in sorghum may be due to the relatively low sampling effort in that habitat. Likewise, the higher species richness in borders of sugar cane compared with that found in the cultivar may be an artifact of the difference in sampling effort.

Peridomestic habitat was distinct in being dominated by *R. rattus* (81% of captures). Part of this difference may be due to the use of rat-size Tomahawk traps in that habitat type. In addition, *R. rattus*, once established in peridomestic habitats, may aggressively defend these habitats against colonization by other species (A. Utrera, in litt.).

The structure of the small-mammal community in our study area was different from that observed during other studies on the llanos. In relatively undisturbed ''bajío'' habitat (within lowland savanna) at Masaguaral, Guárico State (on the central llanos east of our study sites), the small-mammal assemblage was dominated by *Z. brevicauda* (O'Connell 1989; Vivas 1986) or *Marmosa robinsoni* (August 1984). *Rhipidomys* was present (4–6% of captures), and *S. alstoni* was rare (3–4% of captures—August 1984; O'Connell 1989). In contrast, we did not capture *Rhipidomys*, and *S. alstoni* was numerically dominant in all vegetative formations except *Paspalum* savanna. These differences in the small-mammal assemblage could be due to differences in geographic location, habitat, methodology of sampling, or changes in community structure over time.

Different sampling methodologies might account for some differences in capture success for certain species. For example, at Masaguaral, traps placed in trees were more successful at capturing *Marmosa* (P. August, pers. comm.). We rarely placed traps in trees. Vivas (1986) noted an apparent cline in the density of *S. alstoni* and hypothesized that this species may be better adapted to the higher llanos (Barinas and Portuguesa) and is near the geographic and ecologic edge of its distribution on the lower savanna (Guárico and Apure). Some of these possibilities might be eliminated by comparison with our study sites on the ''lower llanos'' of Apure and Guárico. One of our sites (Palo Seco) was in *Trachypogon* savanna about 65 km northeast of Masaguaral. During 300 trap nights in pasture and harvested sorghum at Palo Seco, we captured 30 *S. alstoni*, 9 *Z. brevicauda*, and 2 *S. hispidus*. This assemblage is similar to the small-mammal assemblage at our trapping sites in eastern Apure (Caño la Pica in *Trachypogon* savanna, 60% *S. alstoni*, 40% *Z. brevicauda*; Achaguas in lowland savanna, 55% *S. alstoni*, 45% *Z. brevicauda*; Centro de Recría in lowland savanna, 78% *S. alstoni*, 22% *Z. brevicauda*) and still is in contrast to the *Z. brevicauda–Marmosa*-dominated community at Masaguaral. Thus, observed differences in structure of the small-mammal assemblages are not likely due to differences in geographic locality or vegetative formation, and *S. alstoni* was not more common on the ''higher llanos'' of Barinas and Portuguesa. Increased densities of *S. alstoni* may have occurred in response to agriculture. Although there are no studies evaluating *S. alstoni* as a crop pest, *Sigmodon* species are important pests of a variety of tropical crops, including corn, rice, and sugar cane (Fiedler and Fall 1994). Additional studies are needed to determine whether observed differences in assemblages are due to specific habitat (agriculture versus more natural habitats) or to changes in the small-mammal assemblage over time.

Three rodent species on the western llanos (including the 2 most common species) are reservoirs for disease agents, including Guanarito virus, etiologic agent of Venezuelan hemorrhagic fever. Our data concerning distribution and relative densities of these species among various human-use areas may be of practical importance in risk assessment or development of control strategies to reduce risk of human disease on the western llanos. For example, the apparent preference of *Z. brevicauda* for dense, grassy, perturbed habitats suggests that periodic burning or cutting of this vegetation, especially in peridomestic areas, may decrease the incidence of Venezuelan hemorrhagic fever.

In any analysis of community structure, temporal (seasonal or annual) differences are a potential confounding factor. We minimized seasonal bias by limiting analyses among habitats and land-use categories to areas where sampling was continuous. Diminishing sample sizes and absence of some habitats during some seasons (e.g., the absence of most crop systems during the dry season) make further subdivision of the data impractical.

In summary, the structure of small-mammal assemblages in agricultural and pastoral areas of the western llanos varied among natural vegetative types, habitat types or land-use categories, and specific agricultural systems. Alteration of the environment for human use apparently has resulted in significant changes in the small-mammal assemblages in those environments. The structure of the small-mammal assemblage at a particular site on the western llanos depends on the land-use category and may vary according to the overall vegetative type in which sites are found and according to the specific crop grown. A complete explanation for these differences will depend upon completion of detailed studies elucidating habitat requirements and competitive relationships of individual small-mammal species.

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