

PATTERNS IN THE DIET OF *Sigmodon hispidus* (RODENTIA: CRICETIDAE) IN RELATION TO AVAILABLE RESOURCES IN A TROPICAL SAVANNA

PATRONES EN LA DIETA DE *Sigmodon hispidus* (RODENTIA: CRICETIDAE) EN RELACION A LA DISPONIBILIDAD DE RECURSOS EN UNA SABANA TROPICAL

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ABSTRACT

The diet of *Sigmodon hispidus* was examined by fecal analysis during the dry and wet seasons in a tropical savanna community in Venezuela. A total of 21 plant species were identified in feces out of 42 species in the community. Plant availability as determined by quadrat analysis changed seasonally with the grasses increasing in the rainy season from 70.5 % of all plants to 87.1 % in the dry season. Dicots decreased from the rainy to the dry season. *S. hispidus* had 66.4 % and 33.6 % of its diet made up by monocots and dicots respectively, with grasses and legumes plus composites predominating.

Grasses represented 60.1 % of all consumption in the rainy season, and decreased to 43.2 % in the transition, to increase again to 95.8 % in the dry season. Dicot consumption increased to 57.7 % during the transition, versus 39.9 % and 4.2 % in the rainy and dry season respectively. Few species were preferred, mainly legumes and composites, suggesting that *S. hispidus* balances its diet all year around obtaining most of its nutrients from these few species, plus the grasses. The hypothesis that food availability may be an important factor in population regulation of *S. hispidus* is advanced.

Key Words: rodent diets, tropical rodents, foraging, *Sigmodon hispidus*, llanos, Venezuela.

RESUMEN

La dieta de *Sigmodon hispidus* fue examinada mediante análisis fecales durante las estaciones seca y lluviosa en una comunidad de sabana en Venezuela. Un total de 21 de 42 especies de plantas fueron identificadas en las heces. La disponibilidad de las plantas, determinada por análisis de cuadratas, cambió estacionalmente, con las gramíneas aumentando de 70,5 % de todas las plantas en la estación lluviosa a 87,1 % en la estación seca. Las monocotiledóneas disminuyeron de la estación lluviosa a la estación seca. La dieta de *S. hispidus* estuvo constituida por 66,4 % de monocotiledóneas y 33,6 % de dicotiledóneas, con las gramíneas, compuestas y leguminosas predominando.

Las gramíneas representaron el 60,1 % del total consumido en la estación lluviosa, y disminuyeron a 43,2 % en la época de transición, para aumentar a 95,8 % en la época de sequía. El consumo de dicotiledóneas fue de 39,9 % en la época de lluvias, 57,7 % en el período de transición, y de 4,2 %

en la época de sequía. Pocas especies de plantas fueron preferidas, entre ellas algunas leguminosas y compuestas, sugiriendo que *S. hispidus* balancea su dieta durante el año obteniendo nutrientes de estas pocas especies y de las gramíneas. Se postula la hipótesis de que la disponibilidad de alimentos puede ser un factor importante en la regulación poblacional de *S. hispidus*.

Palabras Claves: dieta de roedores, roedores tropicales, forrageo, *Sigmodon hispidus*, llanos, Venezuela.

INTRODUCTION

Sigmodon hispidus ranges from northern Kansas, in the United States (Cameron 1981; McClenaghan and Gaines 1978) to central Venezuela (Vivas and Calero 1985). Many aspects of its ecology have been studied in the temperate parts of its distribution, but little is known about it in tropical areas except with respect to demography (Ramirez 1972; Ruiz 1985; Vivas and Calero 1985), and reproduction (Durant and Pérez 1982), principally in Venezuela. These studies indicate that *S. hispidus* has yearly density fluctuations with highest densities and reproduction in the rainy season. The pattern of change in rodent biomass closely resembles that of primary production (Vivas and Calero 1985), and the availability of food seems as an important factor limiting density and determining fluctuations of this species in the seasonal tropics. Indirect evidence for this hypothesis is the fact that *S. hispidus* is considered a plague due to its high numbers in corn, sugarcane, pineapple, and rice crops in Venezuela (Aguilera 1985; Ruiz 1985), whereas in natural areas density is low (Ramirez 1972; Vivas and Calero 1985).

Studies of dietary habits have not been carried out for the species in the

tropics. Thus, the main objectives of this study are to determine if: (1) the dietary pattern is related to seasonal availability of resources in natural areas, (2) food might be important as a limiting factor of density in tropical areas, (3) the dietary pattern is similar to that of the species in temperate areas.

STUDY AREA

The area studied was a savanna located within the Estación Biológica de los Llanos, of the Venezuelan Society of Natural Sciences (approximately 300 ha; 8°56'N; 67° 25' W), which has been protected against fire and grazing since 1961. Although some woody vegetation is found (*Byrsonima crassifolia*, *Curatella americana*). The vegetation is basically composed of grasses and forbs including *Trachypogon plumosus*, *Axonopus canescens*, *Hyparrhenia rufa*, *Phaseolus linearis*, and others (Aristiguieta 1976; Monasterio and Sarmiento 1968, 1976; Velasquez 1965). The savanna is becoming more wooded (San-José and Fariñas 1983; Fariñas and San-José 1985), and the fauna may also be changing, as *S. hispidus* was absent in 1968 (Handley 1976; O.A. Reig, personal communication).

The climate is seasonal with a dry season extending from December to May

and a rainy season from May through November (Walter and Medina 1971). The transitions between the two seasons are short and the vegetation changes rapidly, both in composition and cover. Grasses are predominant and their relative importance increases towards the dry season.

MATERIALS AND METHODS

A 10 by 10 grid was established with Sherman traps (23 by 10 by 9 cm) at 10 m intervals, with one trap per station for a total of 100 traps. Traps were baited at sunset with dry oat flakes and sardines and checked at sunrise for a two day period every two weeks (details in Vivas and Calero 1985). Feces were collected each time an animal was caught and the traps were cleaned immediately and every time they were set.

Diet was determined by analysis of feces, which were collected and preserved in FAA until processed, following a slight modification of Stewart's (1967) methodology. Analysis of feces was used instead of the more precise stomach content analysis (Hansson 1970) because it was done within a population dynamics study (Vivas and Calero 1985) and thus, animals could not be sacrificed. The complete fecal sample from each animal was processed and mounted on as many slides as needed. A reference collection of all plants occurring in the study plot was made by processing the plant tissue in the same way as the feces, and was used to identify plant species occurring in the feces.

Fecal samples were analyzed by systematic examination of 20 fields per slide at 100X and counting the particles of each plant species. Frequency of occurrence of each plant species was determined for each fecal sample and was transformed to density assuming that the original data had a Poisson distribution (Sparks and Malecheck 1968). Relative density was determined by dividing the density of each plant species in the diet by the total density and multiplying by 100.

Diets were analyzed by season to assess whether there were seasonal preferences. Seasons were defined as the rainy season (June-November), the transition period (December), and the dry season (January-April), based on rainfall data recorded at the field station meteorological unit. The transition period between the dry and rainy season (May) could not be evaluated because no animals were caught then.

Resource availability was estimated seasonally in 1 m² quadrats whose number was determined from the species-area curve; thus, the majority of the plant species in the area were sampled. The quadrats were placed at random trap stations, yielding a pseudorandom sample of the vegetation. All microhabitats within the grid were covered by the sampling due to the regular distribution of the trap stations. This sampling scheme also assured the inclusion of places actually visited by the rodents, which increased the chance of estimating the availability of most of the plant species eaten by the rodents. The vegetation was sampled once per season.

Resource availability was measured as an Importance Value for each plant species, and the measure of resource utilization was the relative density of each plant species in the diet as determined from all the fecal samples of the animals caught that season, avoiding duplicate samples from the same individuals. The Importance Value per plant species was determined from measures of density and cover obtained from the 1 m² quadrats (Mueller-Dombois and Ellenberg 1974). It must be noted that we did not include frequency in our Importance Value so it is not identical to that reported by Mueller-Dombois and Ellenberg 1974. The Importance Value as we used it is only a relative measure of availability within seasons and the impression that grasses or any other plant category that has a higher value in one season than another does not imply that the particular plant was more available in the season with a higher Importance Value. Biomass may be better as an availability indicator, but we only have monthly averages for all the vegetation (Vivas and Calero 1985)

which are not amenable to a preference analysis as needed in this study.

A Preference Index was used to detect the relationship between the relative density of a plant species in the diet and the availability of the species in the habitat (Hobbs 1982). The Preference Index is determined by dividing the percent of a plant food species in the animals diet by the availability of the plant species in the habitat. A preference index of 1.0 indicates no preference while a value smaller than 1.0 indicates rejection and one larger than 1.0 indicates preference. Availability here is represented by averaging cover and density percentages (Index of Importance) per species across all 1 m² quadrats per season. Standard errors were calculated.

RESULTS

Forty two plant species were available in the area throughout the year, of which twenty one were identified in the diet of *S. hispidus*. Table 1 shows

TABLE 1. Seasonal availability of plants expressed as percentage of importance value, discriminated by family, at the Estación Biológica de los Llanos.

| Family | Rainy Season | Transition Period | Dry Season | Annual Mean |
|------------|--------------|-------------------|------------|-------------|
| Poaceae | 70.5 | 74.6 | 87.1 | 77.4 + 8.7 |
| Asteraceae | 7.7 | 10.1 | 3.3 | 7.0 + 3.5 |
| Fabaceae | 1.8 | 0.8 | 1.1 | 1.2 + 0.5 |
| Labiatae | 14.1 | 10.7 | 6.2 | 10.4 + 4.0 |
| Totals | 94.1 | 96.3 | 97.7 | 96.0 |

seasonal availability of the most common plant families. Resource availability was highest in the rainy season and lowest in the dry season, in both number of plant species (32 in the rainy season, 30 in the transition period, and 15 in the dry season) and importance (Table 1). During the rainy and transition seasons the grasses have the highest Importance Values, along with labiates and composites. In the dry season the grasses are most important. The Importance Value of the grasses increases from 70.5 % in the rainy season to 87.1 % in the dry season (Table 1), indicating that the rodents have fewer choices of diet items in the dry season given that the number of species of grasses is about the same, and that of the dicots decreases drastically.

Utilization of plant resources also varies seasonally (Table 2). Grasses are consumed in high quantities in the rainy season (65 %) and increases to 97 % in the dry season. However, dicots are consumed more in the transition period (57.7 %) even though their availability was only of 24 %. At the species level, *H. rufa* was the most frequently consumed monocot during the rainy and transition seasons, but it was not consumed in the dry season, when it dries out completely by February. *A. canescens* and *T. plumosus* are consumed all year around in low percentages. The most common food at all seasons were grass leaves, including *Hyparrhenia rufa*, *Axonopus canescens* and *Trachypogon plumosus* in that order. The only plants other than grasses consumed in any quantity were the labiates (*Hyptis sp.*),

legumes (e.g., *Desmodium canum* and *Phaseolus linearis*) and the composites (*Spiracantea sp.*, *Vernonia remotiflora*, and an unidentified herb).

Quantitative data on the species of plant consumed must be taken cautiously given that there was relatively low identifiability. Thus, the preference indices only give a rough idea of preference. However, trends for monocots and dicots as groups are reliable since it was always possible to assign all observable material to either category.

DISCUSSION

The diet of *S. hispidus* at the Estación Biológica de los Llanos was composed primarily of grasses, legumes and labiates. We did not find evidence that *S. hispidus* consumes either insects nor seeds. However, we did not make any comparable effort to detect these categories as we did for leaves, primarily because there are no taxonomic studies on which we could rely. Insects are probably consumed and there is a great abundance of them in the rainy and transition periods compared to the dry season, as indicated by a parallel insect diversity study (Vivas, unpublished). Seeds are probably consumed, and they are available all year around as there are six phenological groups of plants which behave differently and set seed throughout the year (Monasterio and Sarmiento 1976). Kincaid and Cameron (1982) report that *S. hispidus* consumed 10 % insects and 5 % seeds in the coastal prairies of Texas.

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TABLE 2. Seasonal dietary composition for *S. hispidus* expressed as relative percent (X) in the diet and the corresponding preference index (PI) for each plant species consumed. Availability of each plant consumed is shown, expressed as a % importance value (Y). Sample sizes in parenthesis (X,Y). a = species preferred even at low availability. b = species rejected at low availability.

| Family | Rainy (16,25) Season | | | Transition (6,30) Period | | | Dry (7,18) Season | | |
|---------------------------------|-------------------------|------|------|-----------------------------|------|------|----------------------|------|------|
| | X | Y | PI | X | Y | PI | X | Y | PI |
| Aesclepiadeaceae | | | | | | | | | |
| <i>Cynanchum sp.</i> | | | | 2.5 | Tr | a | | | |
| Bignoneaceae | | | | | | | | | |
| <i>Arabidea</i> | | | | 0.2 | Tr | a | | | |
| Asteraceae | | | | | | | | | |
| <i>Spiracantea sp.</i> | 0.1 | Tr | a | | | | | | |
| Unidentified herb | 3.8 | 5.8 | 0.7 | | | | | | |
| <i>Vernonia remotiflora</i> | 0.9 | 0.7 | 1.3 | 2.5 | 2.2 | 1.1 | | | |
| Convolvulaceae | | | | | | | | | |
| <i>Evolvulus sericeus</i> | 0.2 | Tr | a | | | | | | |
| Labiataeae | | | | | | | | | |
| <i>Hyptis sp</i> | | | | | | | 2.3 | 6.2 | 0.4 |
| Fabaceae | | | | | | | | | |
| <i>Cassia hispidula</i> | 2.4 | Tr | | | | | | | |
| <i>Desmodium canum</i> | 5.1 | 0.9 | 6.3 | | | | | | |
| <i>Indigosfera pascuorum</i> | 0.2 | 0.2 | 1.0 | 0.2 | 0.2 | 1.0 | 0.2 | 0.2 | 1.0 |
| <i>Phaseolus linearis</i> | 0.1 | Tr | a | 0.5 | 0.1 | 5.0 | | | |
| <i>Theramnus uncinatus</i> | | | | 0.3 | Tr | a | | | |
| Others | 2.4 | | | 17.3 | | | | | |
| Malpighiaceae | | | | | | | | | |
| <i>Byrsonima crassifolia</i> | 0.1 | 0.3 | 0.3 | | | | | | |
| Unidentified dicots | | | | | | | | | |
| Fragments | 24.6 | | | 34.2 | | | 1.7 | | |
| POOLED DICOTS | 39.9 | 28.3 | 1.4 | 57.7 | 24.2 | 2.4 | 4.2 | 10.8 | 0.4 |
| Cyperaceae | | | | | | | | | |
| <i>Bulbostylis capillaris</i> | | | | | | | 0.3 | 3.7 | 0.1 |
| <i>Fimbristyllis dichrotona</i> | 0.1 | Tr | | | | | | | |
| Poaceae | | | | | | | | | |
| <i>Aristida capillacea</i> | 0.5 | 9.4 | 0.05 | | | | | | |
| <i>Axonopus anceps</i> | 0.1 | 2.5 | 0.05 | | | | | | |
| <i>Axonopus canescens</i> | 2.2 | 38.2 | 0.58 | 0.2 | 36.0 | 0.01 | 1.1 | 38.4 | 0.03 |
| <i>Hyparrhenia rufa</i> | 15.0 | 9.4 | 1.7 | 4.0 | 16.2 | 0.3 | | | |
| <i>Laciasis nigra</i> | 0.2 | 0.5 | 0.4 | | | | | | |
| <i>Trachypogon plumosus</i> | 1.6 | 7.6 | 0.2 | 0.2 | 8.5 | 0.02 | 0.4 | 12.8 | 0.03 |
| Unidentified monocots | 40.5 | | | 38.8 | | | 94.0 | | |
| POOLED MONOCOTS | 60.1 | 70.5 | 0.85 | 43.2 | 75.8 | 0.57 | 95.8 | 87.1 | 1.1 |

Monocots were the most abundant resource in the study area (77.4 %) whereas the dicots were available in much lower quantities (21.1 %). Among the monocots, the grasses were the most abundant, varying from species to species, and among the dicots the labiates, composites and legumes were the most abundant (10.4, 7.0 and 1.2 % respectively). These four families comprised around 96 % of all available plants, whereas the other 14 families only represented 4 % of the availability. The pattern was seasonally consistent; the seasonal differences in availability were primarily within families, due to variation in the importance of each species. Thus, seasonal differences in diet composition of *S. hispidus* can be accounted for, to a high degree, by seasonal differences in plant availability. The results generally indicate that *S. hispidus* in the tropics is mainly an herbivore, as found in temperate areas (Flehart and Olson 1969; Kincaid and Cameron 1982).

Within the diet, distinct preferences and avoidances were found. Legumes and composites were always highly preferred, even though their availability was very low. Grasses were highly available and consumed, but few preferences were shown, except for *H. rufa* which was preferred during the rainy season, probably because its greater availability and much larger size than other grasses. All the other plant species showed low preference indices. However, we are reluctant to indicate rejection, even when values of preference are very low, due to the large amount of particles that we could not identify to species. *A. canescens* and *T. plumosus*

probably fall in that category. We hypothesize that *S. hispidus* may somewhat balance its diet all year around by consuming grasses and dicots especially legumes and composites (although we have no real evidence to support this statement, other than the fact that legumes have at least twice the protein content than grasses). Certain variations are found in the pattern: dicots are preferred in the rainy and transition periods. *S. hispidus* might be preferring dicots in the transition period because being of small size and a nonruminant, they should select materials of higher nutritive value which will ferment faster (Parra 1978).

The pattern in diet and preference of dietary items may be explained by Stenseth's et al (1977) hypothesis of optimal diets. In essence, the prediction from their theory would be that the dicots are preferred in the rainy and transition periods because they are readily available and provide at least twice as much protein per unit weight as do grasses (National Academy of Sciences 1979). In the dry season, dicots are not abundant and are probably too dry to be of any use, so *S. hispidus* must consume grasses because they are easily found, although many are dry, except for sprouts of *T. plumosus* and *A. canescens*. The energetic expense of searching for dicots may be too high to warrant actively looking for them. Thus, they end up consuming mainly grasses in the dry season, and eating dicots only if found and not dry.

All seems to indicate that, whereas *S. hispidus* populations are probably not

regulated by food in the temperate areas (Flehart and Olson 1969; Kincaid and Cameron 1982; Cameron 1977), the opposite may be true in the seasonal tropics (Vivas and Calero 1985). Evidence consistent with this hypothesis includes the close relationship between population density and primary productivity in the same rodent population of this study (Vivas and Calero 1985). Also, the data presented in this study may be indicating that scarcity of food in the dry season may be limiting the population of *S. hispidus* in the Venezuelan llanos: only a few species of plants are left and most of these are grasses and are mainly dry. Nutrient concentration in *A. canescens* and *T. plumosus* during the dry season is low compared to that in the rainy season (Montes, unpublished data) and *H. rufa* shows the same pattern (Cruces 1977).

Studies of dietary habits of other New World tropical rodents are scarce. To our knowledge only a few other tropical rodent species have been studied. *Holochilus brasiliensis* consumes mainly rice when it lives in the rice fields, but it is not known what it eats in its natural environment (Cabrera 1984; Martino 1985). *Kerodon rupestris* features partial preferences for certain dietary items, probably because of some micronutrients present in those items (Lacher et al. 1984). *Hydrochoerus hydrochaeris* also shows preferences (Escobar and Gonzalez-Jimenez 1976), although due to its extremely large size and its aquatic habits it is not comparable to any other rodent. *Zygodontomys brevicauda* and *Sigmodon alstoni* (Vivas et al. unpublished) consume mainly plant

material including many seeds. Thus, the information on tropical rodents is so scarce that it is premature to attempt generalizations.

ACKNOWLEDGEMENTS

CONICIT (grant S1-1205) funded most of this study. The Sociedad Venezolana de Ciencias Naturales, and especially Dr. J. J. San-José, provided logistical support and gave permission to work in the field station. Dr. J. J. San-José was very encouraging. Ananías Escalante and Judith Añez helped in the field on several occasions. Dr. Guy Cameron read an early draft and suggested the use of Preference Indices over Diversity Indices, his comments greatly improved the manuscript. Dr. Carlos Bosque, Ricardo Molinet, and Isaac Goldstein, read a later draft and made valuable suggestions. An anonymous reviewer made very valuable comments that further improved the manuscript.

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