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Trophic relationships among four cricetid rodents in rice fields

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Abstract: The food habits of *Holochilus venezuelae, Oryzomys delicatus, Sigmodon alstoni* and *Zygodontomys microtinus* were studied by stomach contents analysis in aged Venezuelan rice-fields. *H. venezuelae* is mainly herbivorous, feeding primarly on rice. The importance of other food items depends on their availability. *S. alstoni*, is omnivorous, its diet consisting of rice seeds (40%) and invertebrates (27%). *O. delicatus* is granivorous, and *Z. microtinus* is chiefly insectivorous (70.6%). Diet diversity (Shannon-Weaver index) is low in *H. venezuelae, O. delicatus* and *Z. microtinus* while *S. alstoni* has high values. All species presented medium to low niche width values (Petraitis Index) in all crop stages. The values for Hom's index of niche overlap between rodent species became greater with food availability. Only *S. alstoni* and *Z. microtinus* seemed to interact significantly when food availability was low. Diets of the four species were related to crop developmental stage, vegetation composition, and characteristics of the habitat surrounding the crop.

Key words: rodent, rice-field, *Holochilus, Sigmodon, Oryzomys, Zygodontomys*, trophic relationships.

Over the last decade, research on communities of small terrestrial mammals has been increasingly focussed on spatial patterns (Dueser and Shugart 1979, M'Closkey 1980, Meserve 1981a, Ostfeld *et al.* 1985, Seagle 1985) and food resource utilization (Hubert and Adams 1981, Kinkaid and Cameron 1982a, Butet 1986).

In turn, trophic studies have been centered (Flake 1973, Kinkaid and Cameron 1982a,b, Meserve 1981a, Rodgers and Lewis 1986)not only in descriptions of ingested food, but also on caloric and energetic requirements (Chew and Chew 1970, Soholt 1973). Optimization feeding models have been propossed (Reichman 1977, Rau *et al.* 1981). Nevertheless, studies dealing with multiple species trophic relationships have been limited because of difficulties in: a) identifying stomach contents (mainly in herbivores and frugivores) and, b) obtaining adequate sample sizes (Meserve 1981b).

Current research in feeding ecology tries to answer mainly three questions: a) how related species in the same habitat could share food resources? (Reichman 1977, Flake 1973, Houtcooper 1978), b) what are the trophic relationships between species? (Meserve 1981b, Meserve 1988), c) is competition for food resources one of the interactions that affect community assemblages? (Smartt 1978, Brown and Liebermann 1973, Trombuleck 1985). Most of these research has been done in natural habitats, but it will be interesting to know the pattern of food resource utilization in less complex ecosystems, such as agrosystems. Althought agrosystems seem evidently uniform and stable, they suffer periodical changes caused by crop cycles. such changes would be reflected on dispersion patterns of the small mammal fauna living there, as well as in their habitat and/or food resource utilization (Barrett *et al*. 1990).

In Venezuela, one of the most common neotropical crops is rice (*Oryza sativa*). A cricetid rodent community (*Holochilus venezuelae, Sigmodon alstoni* and *Oryzomys delicatus*) was found in association with rice-fields in the country (Cartaya and Aguilera 1985), but information on population biology and food habits for the involved species is scarce. Some of them are considered pests in many South American regions (Hershkovitz 1955, Massoia 1974, Twigg 1965). In Venezuela, *H. venezuelae, S. alstoni* and *Zygodontomys microtinus* are considered rice-field pests (Aguilera 1985, Cartaya and Aguilera 1985).

Under this scenario, the objectives of the present study were: 1) to obtain food habit information on *H. venezuelae, S. alstoni* and *O. delicatus,* 2) to relate diet variations with potential food resources in different growth stages of rice crops and 3) to establish trophic relationships between the rodent species found in the rice-field.

MATERIAL AND METHODS

Study area: The study was conducted in two rice plantations near Acarigua city, in Portuguesa State (Venezuela): Los Mamones (9°23'3"N, 69°2'10"W), and El Porvenir (9°23'37"N, 68°53'16"W). Annual temperature in the region was 22-29° C, and mean annual precipitation was 1400 mm with a marked dry season from December to April. rice in different stages of development was the dominant vegetation in both sites. On river and stream banks, a minimal amount of natural vegetation was maintained.

Methods: Sampling took place between July 1983 and April 1984, with one sampling period per month. Two sampling periods (a and b) on each crop stage of development were made. Phase I: between the end of the active vegetative phase and the beginning of the slow vegetative phase (crop age: 1 month); Phase II: Slow vegetative phase (crop age: 2 months); Phase II: Reproductive phase and ripening of rice grain (crop age: 3 months) (Fig. 1).

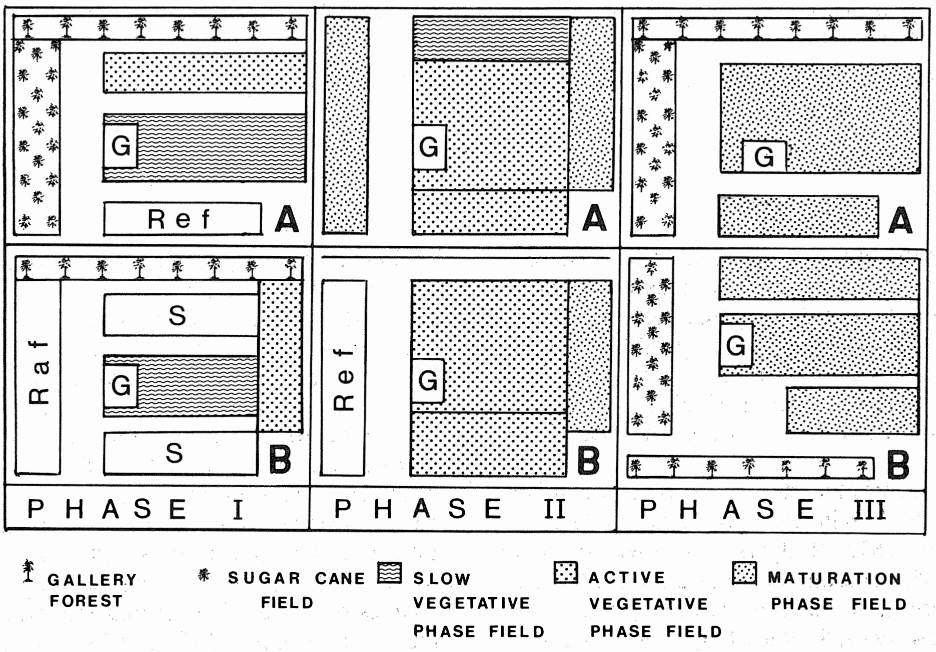

Fig. 1. Grid location in the study area. Letters A and B point out the state of development of adjacent rice-fields at a given sampling period. Ref: Reaped field; Raf: Raked field; G: grid; S: Sown ground.

One trapping grid with 256 stations (15 m spacing) with two snap traps (17.3 x 8.5 cm and 9.0 x 4.6 cm) per station was established in each sampling period of rice field. Traps were baited with a mixture of oatmeal and sardine and checked twice nightly for five nights each month. Standard autopsy data (weight, sex and reproductive condition) were recorded; whole stomachs were removed and fixed in 5% formalin.

Analysis of stomach contents followed standard procedures (Dusi 1949). Subsamples from each stomach were processed and five slides were prepared per subsample; 20 randomly located fields per slide were examined at 100x using a microscope. Frequency and volume percentage (mean percent area occupied per fragments in the microscopic field) were determined. Identification was made with a photomicrograph key prepared from reference slides of the plants and invertebrates found in the study area (see also Martino and Aguilera 1989).

Vegetation cover was analyzed by the point interception method (Mueller-Dumbois and Ellemberg 1974). The survey made in each area of the rice field was slightly different: into the crop area 20 random plots of 1 m^2 were chosen, while in the dams, 0.25 m^2 plots, 10 m apart, were examined along the dam border. In both cases, recording of plant coverage data ceased when the species-area curve stabilized horizontally.

Diet diversity was estimated with the Shannon-Weaver diversity index (H') both for plant parts (H'p) and species (H's) ingested. Plant resoruse niche width was estimated with the Petraitis index (Pi) (Petraitis 1979), which shows very small bias when few resources are abundant, as in our case. Invertebrates were not included in the niche width calculations because their availability was not quantified.

In order to establish trophic relationships between species, niche overlap was calculated using a modification of Morisitas index ($C\lambda$) (Horn 1966), calculated for plant part ingested ($C\lambda p$) and for the whole plant ingested ($C\lambda$ s).

Parametric and non parametric ANOVAS were used to test differences on diet between species and/or samplings periods.

TABLE 1

Species composition and number of animals captured in the several sampling phases at a rice-platation. Roman numbers indicate crop phases, letters denote sampling periods

Species	I		II		III		Total	
	a	b	a	b	a	b	N	%
H. venezuelae	40	111	15	19	101	103	389	82.2
Z. microtinus	0	31	0	0	0	0	31	6.6
S, alstoni	2	11	0	0	7	11	31	6.6
O. delicatus	2	8	1	0	1	10	22	4.6
							483	100.0

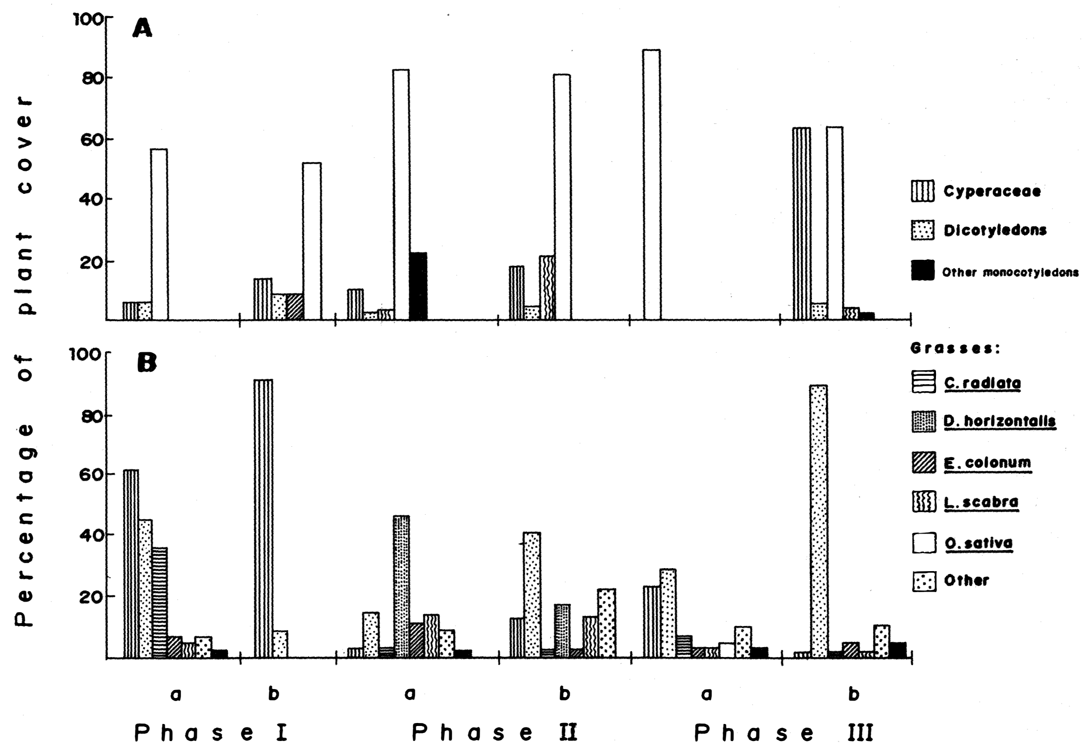

Fig. 2. Percentage of plant coverage of the different species and/or plant groups found in the study area. A: Crop or cultivated area. B: Dam. Sampling periods are denoted by letters a and b.

RESULTS

Animal and plant species composition: *H.venezuelae* was the most common species in all crop phases; the others reached low percentages and were not caught in all crop phases (Table 1). *S. alstoni, O. delicatus* and *Z. microtinus* were almost exclusively captured on dams and/or dry areas of the crop when flooding was minimal, while *H. venezuelae* was trapped in all the grid area. The plant species composition in crop area was different from that found in dams ($p < 0.05$)(Fig. 2). A total of 47 plant species was recorded. In Phase I, rice covered, into the crop area, about 50%. Water, bare ground, and weeds comprised the remaining (Fig. 2A). among weeds, *Cyperus iria* (Cyperaceae) reached the highest coverage value (8%).

During Phase II rice was approaching its maximum vegetative growth and coverage increased (Fig. 2A). weed coverage also increased: *Saggitaria planitiana* (Monocotyledoneae) and *Leptochloa scabra* (Graminae) covered 21% each, and *C. iria* a lower percentage (16%).

In Phase III, weed coverage increased, *Fimbristilis miliacea* (Cyperaceae) reached 62% in period IIIb, while rice coverage was maintained or tended to decline in comparison with Phase II. In all phases dicotyledons were scarce and most species found were small semiaquatic plants.

On dams, species abundance and composition were greater and more variable (Fig. 2B). The usually predominant group was dicotyledons, with exception in sampling periods Ia, Ib and IIa. Coverage of Cyperaceae was generally low, excluding Phase I, when it was almost 90% (Fig. 2B).

The abundance and importance of grass species were also variable: in Phase I *Chloris radiata* coverage was high (sampling period Ia), in Phase II *Digitaria horizontalis* was the dominan grass, and in Phase III there was no dominance.

TABLE 2

Diet composition of four species of cricetid rodents captured in rice fields in Venezuela. Result are expressed in percentage volume with standard deviation in parenthesis (t= traces: < 0.1%)

Items	*H.venezuelae*	*O.delicatus*	*S.alstoni*	*Z.microtinus*
	N= 202	N= 13	N= 24	N=17
Grasses	84.3 (1.4)	76.3 (7.7)	57.8 (5.8)	24.3 (7.0)
O. sativa	66.5 (1.9)	0.8 (0.4)	1.1 (0.4)	1.0 (0.8)
Stems	28.6 (1.7)	5.5 (4.2)	9.2 (3.0)	4.8 (4.7)
Seeds	24.9 (1.9)	63.9 (10.0)	35.8 (6.1)	15.8 (5.2)
L. scabra	5.4 (0.9)	3.0 (2.1)	1.0 (0.5)	
Stems	2.0 (0.3)		0.6 (0.4)	
Bracts	2.6 (0.8)	1.0 (1.0)	0.4 (0.2)	
E. colonum	1.1 (0.4)		3.3 (2.6)	
Stems	0.1 (0.04)			
C. radiata	1.1 (0.4)		0.4 (0.2)	
Stems	0.4 (0.1)		0.1 (0.1)	
S. halepense	0.8 (0.4)	0.4 (0.4)	t	2.1 (1.1)
Leaves	0.4 (0.2)			t
Seeds	0.2 (0.2)	0.4 (0.4)		2.1 (1.1)
D. horizontalis	0.3 (0.1)		1.4 (1.3)	
I. rugosum	0.2 (0.04)	0.1 (0.1)	1.4 (1.1)	
C. dactylon (stems)	0.1 (0.1)		t	
E. punctata	0.1 (0.03)		0.1 (0.1)	
Unidentified	8.9 (0.6)	1.6 (0.9)	2.7 (1.2)	0.4 (0.2)
Cyperaceae	6.0 (1.0)	1.4 (1.0)	6.0 (1.7)	0.1 (0.1)
Cyperus sp.	1.9 (0.5)		0.5 (0.5)	
F. miliacea (seeds)	0.1 (0.03)	0.1 (0.1)	0.5 (0.5)	
Unidentified	4.0 (0.8)	1.3 (0.9)	4.9 (1.4)	0.1 (0.1)
Dicotyledons	1.7 (0.4)	12.6 (6.6)	9.4 (3.3)	4.1 (2.0)
E. alba	0.3 (0.1)		2.3 (1.3)	
Euphorbiaceae	t	5.4 (4.8)	1.1 (0.9)	1.9 (1.2)
Unidentified	1.4 (0.4)	7.2 (4.2)	4.2 (1.6)	2.2 (1.6)
Invertebrates	5.8 (0.8)	6.8 (2.4)	25.9 (6.3)	70.6 (7.2)
Unidentified	1.9 (0.5)	2.9 (1.6)	1.5 (1.1)	1.1 (0.6)

Rodent diet: *H. venezuelae* consumed mainly plant material, particularly grass, followed by Cyperaceae, and dicotyledons; invertebrates were only 5.8% of its diet (Table 2). Rice was the most commonly eaten grass, followed by *L. scabra*, *E. colonum* and *C. radiata* (Table 2). *O. sativa* stems, followed by seeds were the most consumed parts, and considering all grasses, the stems were the item most eaten ($p < 0.0001$). Cyperaceae and dicotyledons were eaten in lower quantities in spite of their abundance in some crops (Table 2 and Fig. 2).

S. alstoni was an omnivorous species. grasses were an important food item, followed by invertebrates, dicotyledons and Cyperaceae (Table 2). Frequency and abundance in which these items were eaten varied significantly ($p<0.05$) from one crop to another (Fig. 3A-C). as in the diet of H. venezuelae, seed consumption increases with crop age.

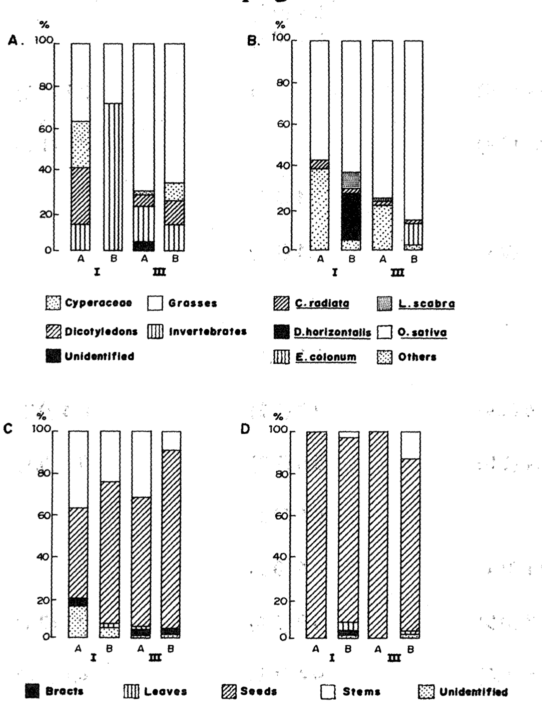

Fig. 3. Percentage of volume of main items ingested by: A: *S. alstoni* per taxa. B: *S. alstoni* per grass species. C: *S. alstoni* per parts of *O. sativa*. D: *O. delicatus*. per parts of *O. sativa*.

O. delicatus was mainly granivorous, its diet included grasses, followed by dicotyledons, Cyperaceae, and invertebrates (Table 2). This species fed primarly on rice seeds (63.9% of total diet). stems and seeds of other grasses, Cyperaceae and dicotyledons, mainly Euphorbiaceae, comprised the remaining items. The proportions of rice seeds in its diet did not differ between sampling periods ($p > 0.1$) (Fig. 3D).

Z. microtinus was mainly insectivorous, its diet consisting of invertebrates, followed by grasses, dicotyledons and Cyperaceae. rice seeds were the main plant material (72% over total rice ingested) followed by *Sorghum halepense* and Euphorbiaceae seeds (Table 2). Grasses were found in 94% of the stomachs analized, rice seeds in 88% of the individuals. all individuals consumed invertebrates. A comparison of diets of the rodent species studied is shown in Fig. 4; differences between their diets were significative ($p < 0.05$).

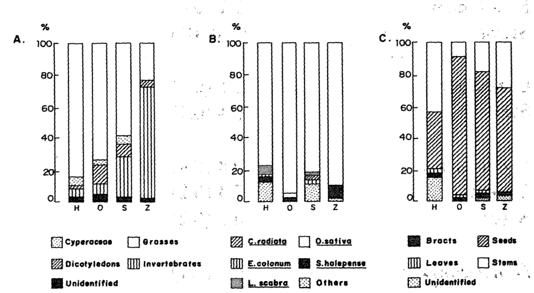

Fig. 4. Percentage of volume of main items ingested by rodent species in the study area. A: per taxa. B: per grass species. C: per parts of *O. sativa*. H: *H. venezuelae*; o: *O. delicatus*; S: *S. alstoni*; Z: *Z. microtinus*.

Diet diversity and niche width: The diet diversity of *H. venezuelae* at H'p level was intermediate (Table 3) and more or less constant throughout rice crop phases. Values for H's were slightly lower. H'p values for *H. venezuelae* were slightly higher than for *S. alstoni* H'p values, but for H's values the situation was inverse. For *O. delicatus*, estimates of both H'were highly variable, ranging from low to intermediate values.

Niche width values (Pi, Table 3) for *H. venezuelae* were intermediate with few variations, low in sampling period Ia and high in sampling period IIIb. *S. alstoni* also shows intermediate Pi values, meaning that their niche width not change throughout the crop phases, in spite of resource variability. *O. delicatus* showed intermediate niche width and *Z. microtinus* showed the highest Pi values, but one of the lowest diet diversities. The reason of this

TABLE 3

Measures of diversity and niche width for rodents in several sampling periods. H'p: Shannon-Weaver diversity index per part of plant (p) and per species of plant (s) ingested. P1: Petraitis niche breadth index. N: Sample size. Roman numbers denote crop phases, letters sampling period

Phases		N	H'p	H's	Pi
H. venezuelae					
I	a	18	1.00	0.72	0.33
	b	46	0.70	0.41	0.75
II	a	12	0.73	0.60	0.77
	b	15	0.90	0.67	0.53
III	a	53	0.76	0.39	0.57
	b	58	0.91	0.55	1.10
O. delicatus					
I	a	2	0.21	0.20	0.59
	b	8	0.90	0.75	0.59
III	a	1	0.03	0.03	0.89
	b	10	0.70	0.19	0.90
S. alstoni					
I	a	2	0.96	0.93	0.28
	b	11	0.49	0.40	1.24
III	a	7	0.82	0.57	0.89
	b	11	0.78	0.66	0.76
Z. microtinus					
I	b	17	0.46	0.39	1.24

result is that Pi measures niche width in relation to availability of plant resources. In this way, rodent species that eat few invertebrates will show subestimate Pi values and vice versa.

Niche overlap: In all stages the $C\lambda p$ index was lower than the $C\lambda s$ index (Table 4). Values of niche overlap estimated for *O. delicatus* versus the other rodent species were high in sampling period Ia for $C \lambda p$, while *S. alstoni* and *Z. microtinus* shared the highest values in period Ib. In IIIa niche values were higher than in period I for all species involved. The lowest overlap values were presented by *O. delicatus* regarding the other species and considering only the plant parts eaten ($C \lambda p$). *H. venezuelae* and *S. alstoni* always shared high values. During IIIb, overlap values were even higher than in the previous crop stage, and similar among rodent species.

DISCUSSION

A summary of trophic relationships described for this rodent community is presented in Fig. 5.

The dominant species was *H. venezuelae*, an herbivorous rodent which can ingest important amounts of animal matter. The importance of plant parts and species consumed varied with crop stage (Martino and Aguilera 1989). Other

TABLE 4

Horn's (1966) niche overlap index (CY) for the four species of rodents studied in different crop phases. Cyp: niche overlap index per part of plant ingested. CYs: niche overlap index per species of plant ingested. Roman numbers denote crop phases, letters sampling periods

Species	Phases		*O. delicatus*		*S. alstoni*		*Z. microtinus*	
			$C\lambda s$	$C\lambda p$	$C\lambda s$	$C\lambda s$	$C\lambda s$	$C\lambda s$
H.venezuelae	I	a	0.73	0.31	0.75	0.70	-	-
		b	0.68	0.06	0.27	0.09	0.31	0.08
	III	a	0.97	0.66	0.94	0.91	-	-
		b	0.95	0.84	0.97	0.97	-	-
O. delicatus	I	a	-	-	0.44	0.21	-	-
		b	-	-	0.29	0.24	0.33	0.28
	III	a	-	-	0.87	0.64	-	-
		b	-	-	0.91	0.91	-	-
S. alstoni	I	b	-	-	-	-	0.99	1.00

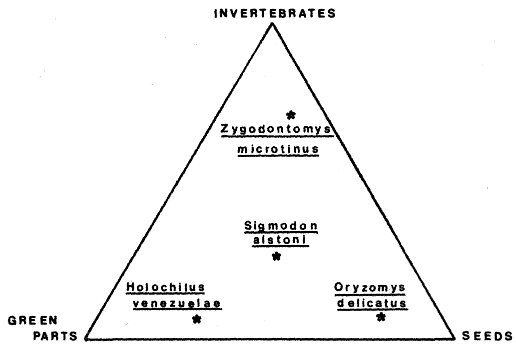

Fig. 5. Trophic realtionships of four species of rodents in rice-fields of Venezuela determined by stomach content analyses. Proximity of points to apexes of triangle denotes relative importance of three major food categories.

Holochilus species were also found to be mainly herbivorous (Hershkovitz 1955, Twigg 1965). Second in importance is *S. alstoni,* which is omnivorous. Related species, like *S. hispidus,* feed primarly on grasses, leaves and seeds during the summer, when invertebrates are less important (Kinkaid and Cameron 1982b, Vivas and Calero 1985, 1988).

O. delicatus was found to be mostly granivorous; values of diet diversity and niche width suggest specialization in the use of this vegetable resource. Other species, like *O. longicaudatus* in Chile, eat primarily seeds during the dry season, and pollen and flowers during the wet season (Meserve 1981a,b, Murua and Gonzalez 1981). *O. palustris texensis* eats seeds, green vegetation (Svihla 1931) and large quantities of insects and crustaceans (Sharp 1967, Kinkaid and Cameron 1982b), both species also showed small niche widths.

Z. microtinus was a sporadic species in this study, since it only occurred in one sampling period (Table 1). It appeared to be strongly insectivorous, but was a generalist in the use of plant resources (see H' and Pi values, Table 3). There is little information about this rodent, and it is not clear if the diet observed is a result of the particular conditions in which it was captured (see Results and Fig. 1). In Guarico state, Vivas (1984) found that *Z. microtinus* eats plant material, but the proportion of this item in the diet is unknown.

Diet variations found during the study could be explained by three factors:

1. Crop developmental stage: This explains differences in item ingestion between the species and seemingly affects mainly *H. venezuelae* and *S. alstoni*, since they eat large amounts of *O. sativa* seeds during advanced crop phases (Phase III, Fig. 3C) where seeds are more available and stems become less palatable (Martino and Aguilera 1989). The stage of development in the rice fields also explains differential rodent catches, as they relate to variations of water level. Such variations á might open potential habitats that could be used temporally by *O. delicatus*, *S. alstoni* and *Z. microtinus*, which are not adapted to semiaquatic habitats. On the other hand, *H. venezuelae* is able to use this environment quite successfully (Hershkovitz 1955). Niche overlap was small in early crop phases, increasing with the stage of the crop, probably because the increase of food resources lead the animals to use them more extensively.

2. Composition of plant species; This factor seems to affect *S. alstoni* more than other species. In crops where dams had abundant vegetation, more dicotyledons were consumed by *S. alstoni*, which had a wide niche; this pattern was not found in crops where vegetation was scarce or nil, (Fig. 1 and Fig. 3A). For *H. venezuelae*, diet composition was mainly affected by variation of percentage of weeds in the crop area (Martino and Aguilera 1989), and the resulting niche width values were high. *O. delicatus* consumed more seeds of Euphorbiaceae when the availability of rice seeds was low (Phase I). These results may be explained by the way these species exploit the horizontal space: *S. alstoni* and *O. delicatus* dwell in dry weedy areas while *H. venezuelae* occupy mainly wet cultivated areas.

3. Surrounding crop area at sampling time: Changes in the vegetation of the surrounding crop area also influence the diet of rodents. The ingestion of seeds, when free-seed crops were sampled, indicate that the animals were feeding in places different from their capture sites. This was also evidenced by the occurrence of plants in stomach conten∫ no∫ found in the grid vegetation survey.

Agrosystems might be used as models of variation in rodent food habits, because they allow a rapid species-response to change inside the ecosystem. Changes could be observed not only in food ingested, but also in habitats shared at a given moment and in niche width and overlap values. These change with environmental conditions, indicating the opportunistic behaviour of these rodents in relation to resource availability. In similar studies in other agrosystems it has also been observed that rodents tend to profit from using resources opportunistically (Houtcooper 1978, Truszkowski 1982).

Finally, this study points out that *H. venezuelae* feeds mainly on stems, followed by seeds of *O. sativa*. Since it is the most abundant rodent species in the study area, its impact on rice field damage could be considerable (Cartaya and Aguilera 1985, Candellet 1984). Damage involves all crop phases, whether the whole plant is destroyed in the early phases by eating stems, or by eating seeds and stems in later phases, which in any case decreases crop production. The other rodent species are less abundant, but they could become pests, especially in phases where seeds are present (Phase III).

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RESUMEN

Mediante análisis de contenidos estomacales, se estudiaron los hábitos alimentarios de *Holochilus venezuelae*, *Oryzomys delicatus*, *Sigmodon alstoni* y *Zygodontomys microtinus*, roedores presentes en diferentes edades de cultivos de arroz en Venezuela. *H. venezuelae* fue principalmente herbívoro, siendo el arroz el mayor renglón consumido. la importancia de otros renglones ingeridos dependió de su disponibilidad en el área de estudio. *S. alstoni* presentó una dieta principalmente omnívora que consistió básicamente en semillas de arroz (40%) e invertebrados (27%). *O. delicatus* fue granívoro y *Z. microtinus* consumió principalmente insectos (70.6%). *H. venezuelae*, *O. de-*

licatus y *Z. microtinus* mostraron baja diversidad de dieta (Indice Shannon-Weaver) mientras que *S. alstoni* presentó valores más altos. Para todas las especies y en todas las edades del cultivo, se encontraron amplitudes de nicho con valores medios a bajos (Indice de Petraitis) y valores de solapamiento de nicho proporcionales a la disponibilidad del alimento. Sólo *S. alstoni* y *Z. microtinus* tendieron a mostrar altas interacciones cuando la disponibilidad del alimento fue baja. Las dietas de todas las especies se relacionan con el estado de desarrollo del cultivo, la composición de la vegetación y las características del área que rodea al cultivo en el momento del muestreo.

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