

Population variability of Neotropical rodents: influence of body size, habitat, and food habits

Variabilidad poblacional de roedores neotropicales: influencia de
tamaño corporal, hábitat y hábitos alimentarios

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ABSTRACT

Population variability of Neotropical rodents is examined with respect to taxon, body mass, habitat association, and trophic category. The coefficient of variation of reported density estimates of local populations is used as a measure of variability. The Cricetid rodents exhibit the greatest range of variability. Larger species are less variable than smaller ones. Populations of rodents from temperate forests and tropical savannas are more variable than those from tropical wet forests. No clear relation between trophic category and population variability is discernible.

Key words: Population variability, Neotropical Region, Rodents.

RESUMEN

La variabilidad poblacional de roedores neotropicales se examina con respecto a taxón, tamaño corporal, asociación al hábitat, y categoría trófica. El coeficiente de variación de las densidades estimadas de poblaciones locales de roedores se usa como estimador de su variabilidad. Los roedores cricétidos exhiben el mayor rango de variabilidad. Las poblaciones de especies grandes son menos variables que las de especies pequeñas. Las poblaciones de roedores de bosques templados y sabanas tropicales son más variables que aquellas de bosques tropicales húmedos. No existe una relación clara entre la categoría trófica y la variabilidad poblacional de roedores.

Palabras claves: Variabilidad poblacional, Región Neotropical, Roedores.

INTRODUCTION

Populations of Neotropical rodents exhibit fluctuations of variable magnitude, but our understanding of the factors underlying these fluctuations is limited due to the dearth of long-term studies. Murua & Gonzalez's (this volume) work on southern Chilean rodents is an exception. They report within—and between—year fluctuations in populations of *Oryzomys longicaudatus* and *Akodon olivaceus* in temperate rain forests. They consider the former species to be an environmental tracker, responding to variations in the seed crop, whereas fluctuations of the latter species are viewed as cyclic, similar to the microtine cycles of the Holarctic. Their results are intriguing, but I think it premature to describe the fluctuations as cyclic, as evi-

denced by the revision of the periodicity of *A. olivaceus* cycles from four years (Murúa & González 1985) to five years (Murúa & González, this volume). Although elucidation of the temporal dynamics of Neotropical small mammal populations must await more long-term studies, the purpose of this paper is to address several broad questions concerning the variability of Neotropical rodent populations. Specifically, I examine patterns in population variability as they relate to taxon, body mass, habitat association, and trophic category.

METHODS

To standardize field estimates of population variability, I used the coefficient of variation (CV) for mean density estimates

of Neotropical rodents as a measure of variability. Comparative density information on these species is summarized in Table 1. All density estimates were based on mark-recapture studies. In four cases, CV's were based on capture frequencies along transects rather than on density estimates (see Table 1). The remainder of the CV's were based on density values obtained from trapping grids. Approximately half of these studies included border strips around the grid for density estimates. The majority of these grid studies expressed population size as the minimum number known alive. Other grid studies used either some statistical estimation of density or simply expressed population size in terms of abundance. Densities expressed in forms other than number/hectare were converted to number/hectare for ease of comparison. Nomenclature follows Honacki *et al.* (1982).

The coefficient of variation of abundance estimates has been used to examine population variability in other vertebrate populations (e.g., Karr 1982). I calculated the CV's for the density estimates using the standard formula: $CV = s \times 100/Y$ (s = standard deviation; Y = mean). Sokal & Rohlf (1981, p. 59) suggest that CV's calculated in this manner might be biased, especially when small sample sizes are involved, and present a corrected estimate: $CV^* = (1 + 1/4n)CV$. The range of sample sizes (= number of censuses) used in the calculation of CV's for the density estimates (Table 1) suggest that this potential bias might be problematical. However, I calculated CV's using both formulae and my results were the same. I consider statistical tests significant at $P < 0.05$.

RESULTS AND DISCUSSION

Mean density estimates ranged from less than one to 97 animals/ha and CV's were from 14 to about 160 (Table 1). Significant correlation of mean and CV would invalidate use of CV, but this was not the case ($r = -0.21$; $df = 71$; ns). The population studies varied considerably in length (Table 1). I determined if the CV and length of study were significantly correlated. One might expect the CV to increase with length of study because longer studies would have a greater likelihood of incorporating population fluctuations. Conversely,

the CV could decrease with length of the study due to the central limit theorem. Although CV exhibited an increase with length of study, the trend was not significant ($r = + 0.20$; $df = 75$; ns).

Relationships between body size and population dynamics have been suggested for a variety of mammalian taxa (e.g., McNab 1980). To examine such a relationship for these Neotropical rodents, CV was plotted against body mass in Figure 1. A significant negative correlation ($r = -0.24$; $df = 75$; $P < 0.05$) was observed, indicating that populations of larger species are less variable. Among the smaller species, a wide range of CV's was observed, suggesting the need to further examine patterns.

The distribution of the CV's between different rodent families are illustrated with respect to habitat association and trophic category in Figures 2 and 3. The family Cricetidae was subdivided with two general, *Oryzomys* and *Akodon*, separated from the other genera because of large sample size. Differences between the mean CV's for the taxa, habitat association, and trophic categories were examined by one-way Analysis of Variance (Table 2).

Most populations studied had CV's less than 100. The greatest variability was observed within the Cricetid species, with CV's ranging from 19.1 to 157.7. Comparison of the different taxa suggested that the mean CV for the Cricetidae was greater than that of other taxa, although the difference was only marginally significant (Table 2). Because of the large sample size of the Cricetids relative to the other taxa, I compared the CV's of the Cricetids with those of all other taxa combined using a t-test for unequal variance (Sokal & Rohlf 1981). This comparison indicated that populations of the Cricetid species were indeed more variable than populations of the other species ($t = 3.78$; $P < 0.05$). Populations from tropical wet forests exhibited the lowest CV's, whereas those from temperate forests and tropical savannahs were significantly larger (Table 2). Fleming (1975) suggested that among tropical habitats, populations of small mammals from tropical grasslands might be less constant than those from tropical forests. These comparisons support his speculations. The mean CV's for the different trophic categories were not significantly different.

TABLE 1

Density estimates and coefficients of variation of these estimates for populations of Neotropical rodents
 Densidades estimadas y coeficientes de variación de dichos estimados para poblaciones de roedores neotropicales

Family/species	Locality/ Habitat	Mass (grams)	Density* (Range)	CV **	Trophic Category***	Length of Study (mo) ⁺	Source
SCIURIDAE							
<i>Sciurus granatensis</i>	Venezuela/ Tropical savanna	250	0.4 ± 0.1 (0.2-0.5)	32.5	FR/GR	26	O'Connell 1981
	Venezuela/Tropical dry forest	250	0.5 ± 0.1 (0.4-0.9)	25.5	FR/GR	16	August 1981
HETEROMYIDAE							
<i>Liomys adspersus</i>	Panama/Tropical dry forest	65	7.9 ± 2.0 (5.4-11.0)	25.6	FR/GR	13	Fleming 1971
<i>L. salvini</i>	Costa Rica/ Tropical dry forest	43	5.9 ± 1.4 (3.9-8.3)	23.7	FR/GR	13	Fleming 1974
<i>Heteromys anomalus</i>	Venezuela/Tropical humid forest	70	1.0 ± 0.8 (0.0-3.0)	74.8	FR/GR	22	O'Connell 1981
	Venezuela/Tropical dry forest	70	1.1 ± 0.7 (0.0-2.2)	65.5	FR/GR	16	August 1981
<i>H. desmarestianus</i>	Costa Rica/ Tropical wet forest	77	13.5 ± 3.1 (6.5-18.3)	23.3	FR/GR	13	Fleming 1974
CRICETIDAE							
<i>Oryzomys bauri</i>	Ecuador - Galapagos/ Tropical desert	65	++	28.0	FR/OM	31 (7)	Clark 1980
<i>O. bicolor</i>	Venezuela/ Tropical savanna	25	0.7 ± 0.4 (0.2-1.2)	61.2	FR/OM	6	August 1981
	Panama/Tropical moist forest	50	2.3 ± 1.3 (0.3-4.3)	57.0	FR/OM	13	Fleming 1971
<i>O. capito</i>	Panama/Tropical dry forest	50	1.1 ± 1.1 (0.0-3.2)	100.0	FR/OM	13	Fleming 1971
	Trinidad/Tropical evergreen forest	60	16.0 ± 3.7 (11.0-21.2)	23.1	FR/OM	9	Everard & Tikasingsh 1973
	Venezuela/Tropical humid forest	60	1.2 ± 1.2 (0.0-3.2)	65.0	FR/OM	22	O'Connell 1981
<i>O. concolor</i>	Venezuela/Tropical humid forest	65	1.3 ± 1.1 (0.3-4.6)	80.0	FR/OM	22	O'Connell 1981
<i>O. eliurus</i>	Brazil/ Tropical savanna	30	9.8 ± 7.3 (3.3-32.0)	74.5	FR/OM	24	Mello 1980
<i>O. longicaudatus</i>	Chile/Temperate scrub grassland	46	4.6 ± 4.0 (0.0-7.6)	87.8	FR/GR	7 (3)	Fulk 1975
	Chile/ Temperate forest	45	5.9 ± 7.4 (0.0-29.6)	125.4	FR/GR	53 (27)	Meserve et al. 1982 + pers. comm.
	Chile/ Temperate forest	45	4.7 ± 5.4 (0.0-16.0)	115.2	FR/GR	16	Meserve et al. 1982 + pers. comm.
	Chile/Temperate rain forest	45	11.8 ± 14.8 (1.0-62.0)	125.2	FR/GR	53 (47)	Murúa et al. in press
	Chile/Temperate grassland	45	11.4 ± 10.4 (1.0-41.0)	91.0	FR/GR	53 (46)	Murúa et al. in press
<i>O. nigripes</i>	Argentina/ Temperate grassland	40	14.7 ± 19.9 (0.0-30.8)	146.7	FR/GR	17 (36)	Dalby 1975
	USA, Louisiana/ Coastal sedge	55	6.6 ± 6.0 (0.5-17.8)	91.7	FR/OM	47 (19)	Negus et al. 1961
<i>O. subflavus</i>	Brazil/ Tropical savanna	40	5.3 ± 2.1 (1.7-9.2)	39.6	FR/OM	12	Valle et al. 1982
<i>Neacomys tenuipes</i>	Venezuela/Tropical humid forest	15	2.6 ± 2.7 (0:10.1)	104.9	FR/OM	22	O'Connell 1981
<i>Rhipidomys mastacalis</i>	Venezuela/Tropical humid forest	100	1.1 ± 1.1 (0.3-5.0)	99.1	FR/OM	22	O'Connell 1981

Family/species	Locality/ Habitat	Mass (grams)	Density* (Range)	CV **	Trophic Category***	Length of Study (mo) [†]	Source
<i>Rhipidomys</i> sp.	Venezuela/ Tropical savanna	80	1.6 ± 1.3 (0.0-5.0)	81.2	FR/OM	26	O'Connell 1981
<i>Thomasomys dorsalis</i>	Brazil/Tropical moist forest	90	++	49.1	FR/GR	9	Davis 1945
<i>Akodon arviculoides</i>	Brazil/Tropical moist forest	35	++	70.4	FR/HB	9	Davis 1945
<i>A. azarae</i>	Argentina/ Temperate grassland	24	97.2 ± 42.0 35.8-178.3)	43.2	FR/HB	17 (36)	Dalby 1975
<i>A. longipilis</i>	Argentina/ Temperate forest	37	3.2 ± 0.61 (2.8-3.9)	19.1	FR/OM	23 (3)	Pearson & Pearson 1982
	Argentina/ Temperate forest	37	5.5 ± 3 (3.1-9.4)	54.6	FR/OM	23 (4)	Pearson & Pearson 1982
	Argentina/ Temperate forest	37	4.4 ± 5.6 (0.4-10.8)	127.3	FR/OM	23 (3)	Pearson & Pearson 1982
	Chile/Temperate scrub grassland	51	7.1 ± 1.7 (4.8-8.7)	23.6	IN/OM	10 (4)	Fulk 1975
	Chile/Temperate scrub grassland	51	2.8 ± 0.8 (1.4-3.6)	28.1	IN/OM	15 (8)	Meserve 1981
	Chile/ Temperate forest	51	11.4 ± 5.8 (0.0-21)	51.0	IN/OM	53 (27)	Meserve <i>et al.</i> 1982 + pers. comm.
	Chile/ Temperate forest	51	12.6 ± 4.1 (6.2-21.0)	32.6	IN/OM	16	Meserve <i>et al.</i> 1982 + pers. comm.
	Chile/Temperate rain forest	51	2.4 ± 3.9 (0.0-24.0)	157.7	IN/OM	53 (47)	Murúa and Meserve pers. comm.
	Chile/Temperate grassland	51	3.5 ± 3.4 (0.0-15.0)	96.8	IN/OM	53 (46)	Murúa and Meserve pers. comm.
<i>A. olivaceus</i>	Argentina/ Temperate forest	25	3.1 ± 3.2 (0.0-7.2)	102.4	FR/OM	23 (4)	Pearson & Pearson 1982
	Chile/Temperate scrub grassland	31	10.5 ± 4.9 (6.3-15.9)	46.7	IN/OM	7 (3)	Fulk 1975
	Chile/Temperate scrub grassland	30	67.2 ± 28.3 (30.3-97.0)	42.1	IN/OM	10 (4)	Fulk 1975
	Chile/Temperate scrub grassland	30	16.5 ± 7.5 (7.1-31.4)	45.2	IN/OM	15 (8)	Meserve 1981
	Chile/ Temperate forest	30	17.6 ± 11.4 (1.2-45.9)	64.8	IN/OM	53 (27)	Meserve <i>et al.</i> 1982 + pers. comm.
	Chile/ Temperate forest	30	29.6 ± 15.4 (11.1-55.6)	52.0	IN/OM	16	Meserve <i>et al.</i> 1982 + pers. comm.
	Chile/Temperate rain forest	30	17.3 ± 15.9 (1.0-60.0)	92.1	IN/OM	53 (46)	Murúa and Meserve pers. comm.
	Chile/Temperate grassland	30	16.1 ± 12.6 (1.0-67.0)	78.2	IN/OM	53 (47)	Murúa and Meserve pers. comm.
<i>A. nigrata</i>	Brazil/Tropical moist forest	40	++	60.6	FR/HB	9	Davis 1945
<i>A. sanborni</i>	Chile/ Temperate forest	30	3.1 ± 3.6 (0.0-16.0)	117.8	IN/OM	53 (27)	Meserve <i>et al.</i> 1982 + pers. comm.
	Chile/ Temperate forest	30	2.6 ± 1.6 (1.2-6.2)	62.0	IN/OM	16	Meserve <i>et al.</i> 1982 + pers. comm.
<i>A. urichi</i>	Venezuela/Tropical humid forest	55	2.9 ± 1.7 (0.6-5.9)	59.0	FR/HB	22	O'Connell 1981
<i>Zygodontomys breviceauda</i>	Venezuela/ Tropical savanna	40	9.8 ± 13.1 (0.0-40.0)	133.7	FR/OM	26	O'Connell 1981
	Venezuela/Tropical dry forest	40	0.6 ± 0.6 (0.0-1.8)	100.0	FR/OM	16	August 1981
<i>Bolomys lasiurus</i> (= <i>Zygodontomys</i>)	Brazil/ Tropical savanna	40	10.7 ± 11.3 (0.0-42.0)	105.6	FR/OM	19	Mello 1980
<i>B. lasiurus</i> (= <i>Zygodontomys</i>)	Brazil/ Tropical savanna	40	8.6 ± 5.6 (1.7-16.7)	64.8	FR/OM	12	Valle <i>et al.</i> 1982
<i>Calomys callosus</i>	Brazil/ Tropical savanna	25	11.1 ± 7.7 (2.7-32.7)	69.6	FR/OM	24	Mello 1980
<i>C. musculinus</i>	Argentina/ Temperate grassland	12	1.9 ± 1.8 (0.0-62.0)	94.7	FR/OM	17 (36)	Dalby 1975
<i>Oxymycterus rutilans</i>	Argentina/ Temperate grassland	90	5.6 ± 2.2 (0.8-24.0)	39.3	IN/OM	17 (36)	Dalby 1975

Family/species	Locality/ Habitat	Mass (grams)	Density* (Range)	CV **	Trophic Category***	Length of Study (mo) ⁺	Source
<i>Irenomys tarsalis</i>	Argentina/ Temperate forest	43	2.9 ± 1.9 (1.4-5.1)	65.5	HB/BR	23 (3)	Pearson & Pearson 1982
<i>Auliscomys micropus</i>	Argentina/ Temperate forest	78	3.7 ± 1.8 (0.0-4.1)	48.6	FR/HB	23 (4)	Pearson & Pearson 1982
<i>Phyllotis darwini</i>	Chile/Temperate scrub grassland	51	41 ± 7.9 (29.4-46)	19.3	FR/GR	10 (4)	Fulk 1975
	Chile/Temperate scrub grassland	50	2.7 ± 1.9 (0.6-4.4)	70.4	FR/GR	7 (3)	Fulk 1975
	Chile/Temperate scrub grassland	50	9.8 ± 6.0 (4.3-21.4)	61.3	FR/GR	15 (8)	Meserve 1981
<i>Holochilus brasiliensis</i>	Argentina/ Temperate grassland	160	3.7 ± 3.5 (0.0-10.7)	94.6	HB/GR	17 (36)	Dalby 1975
<i>Sigmodon alstoni</i>	Venezuela/ Tropical savanna	55	1.5 ± 1.4 (0.0-4.3)	94.2	HB/BR	26	O'Connell 1981
CAVIIDAE							
<i>Microcavia australis</i>	Argentina/ Temperate grassland	360	23.5 ± 7.5 (8.3-33.3)	32.1	HB/GR	11 (8)	Rood 1972
<i>Cavia aperea</i>	Argentina/ Temperate grassland	525	20.6 ± 16.4 (8.3-39.2)	79.8	HB/GR	11 (3)	Rood 1972
OCTODONTIDAE							
<i>Octodon degus</i>	Chile/Temperate scrub grassland	210	3.6 ± 1.3 (2.5-5.0)	36.1	HB/BR	7 (3)	Fulk 1975
	Chile/Temperate scrub grassland	210	29.1 ± 23.5 (6.3-64.2)	81.0	HB/BR	9 (5)	Meserve <i>et al.</i> 1984
	Chile/Temperate scrub grassland	210	34.1 ± 17.4 (10.0-63.0)	51.0	HB/BR	20 (14)	Meserve <i>et al.</i> 1984
	Chile/Temperate scrub grassland	210	21.1 ± 10.5 (11.6-39.2)	50.0	HB/BR	12 (10)	Jaksić <i>et al.</i> 1981
ABROCOMIDAE							
<i>Abrocoma bennetti</i>	Chile/Temperate scrub grassland	275	1.6 ± 1.3 (0.0-3.6)	80.1	FR/HB	15 (8)	Meserve pers. comm
ECHIMYIDAE							
<i>Proechimys guairae</i>	Venezuela/Tropical humid forest	325	4.4 ± 1.1 (2.5-6.1)	25.5	FR/GR	22	O'Connell 1981
<i>P. guyannensis</i>	Trinidad/Tropical evergreen forest	350	10.5 ± 1.5 (9.2-13.0)	13.9	FR/GR	9	Everard & Tikasingsh 1973
<i>P. semispinosus</i>	Panama/Tropical moist forest	280	3.6 ± 1.7 (1.0-5.8)	46.6	FR/GR	13	Fleming 1971
<i>P. semispinosus</i>	Panama/Tropical dry forest	300	2.1 ± 1.3 (0.6-3.9)	61.9	FR/GR	13	Fleming 1971
<i>Thrichomys aperoides</i>	Brazil/Tropical thorn scrub	300	5.4 ± 4.2 (0.0-10.8)	77.8	FR/HB	14	Streilein 1982

* no/ha ± 1 SD

** CV = Coefficient of variation; calculated prior to rounding mean density estimates

*** FR/GR = frugivore/granivore; FR/OM = frugivore/omnivore; IN/OM = insectivore/omnivore; FR/HB = frugivore/herbivore; HB/BR = herbivore/browser; HB/GR = herbivore/grazer.

+ numbers in parentheses refer to number of censuses during study, if not equal to duration of study in months.

++ only capture frequencies available.

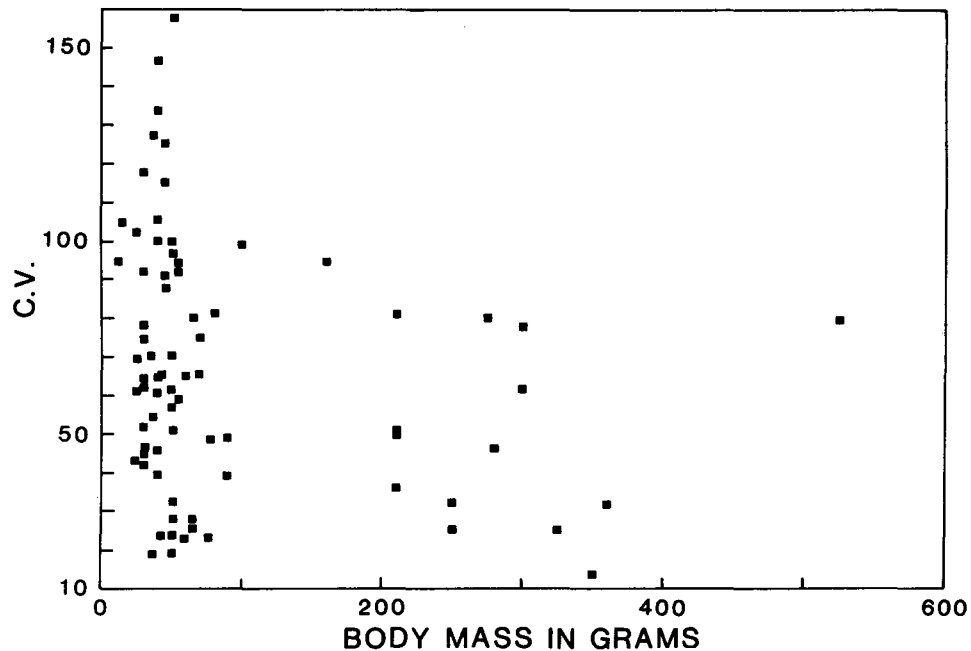


Fig. 1. Coefficient of variation (CV) of density estimates of local population of Neotropical rodents plotted against body mass ($r = -0.24$; $df = 75$; $P < 0.05$).

Coefficientes de variación (CV) de los estimadores de densidad de poblaciones locales de roedores neotropicales graficados contra sus masas corporales ($r = -0.24$; $gl = 75$; $P < 0.05$).

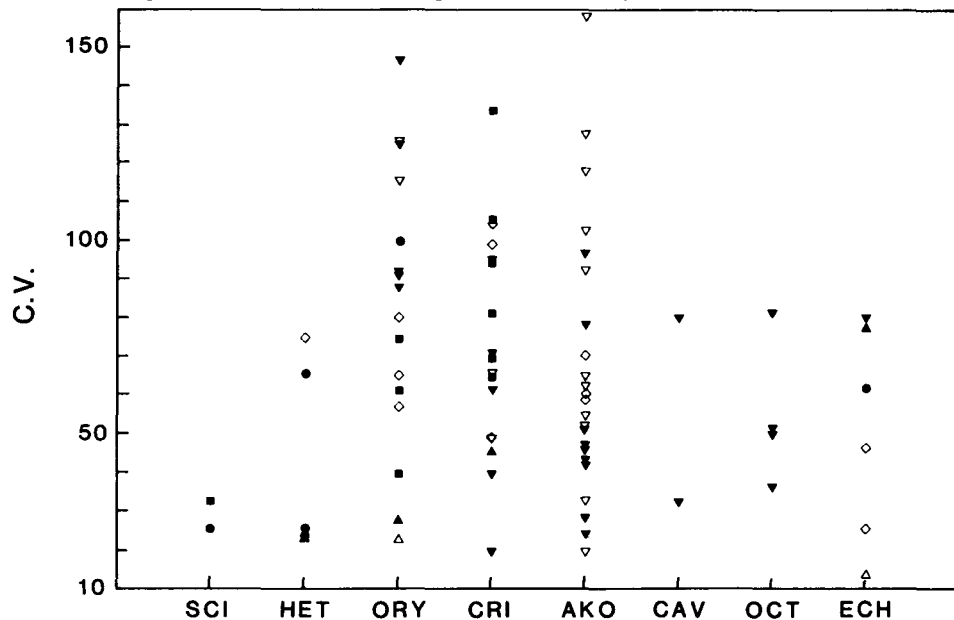


Fig. 2. The relation between coefficient of variation (CV) of density estimates and habitat association for Neotropical rodent taxa. ■ = Tropical savannah; ● = Tropical dry forest; ◇ = Tropical humid forest; △ = Tropical wet forest; ▲ = Tropical desert; ▼ = Temperate grassland; ▽ = Temperate forest. Sci = Scuriidae; Het = Heteromyidae; Ory = *Oryzomys*; Cri = Cricetidae (exclusive of *Oryzomys* and *Akodon*); Ako = *Akodon*; Cav = Caviidae; Oct = Octodontidae; Ech = Echimyidae + Abrocomidae.

Relación entre el coeficiente de variación (CV) de los estimadores de densidad y la asociación al hábitat de roedores neotropicales. ■ = Sabana tropical; ● = Bosque tropical seco ◇ = Bosque tropical húmedo; △ = Bosque tropical perhúmedo; ▲ = Desierto tropical; ▼ = Pradera templada; ▽ = Bosque templado. Sci = Scuriidae; Het = Heteromyidae; Ory = *Oryzomys*; Cri = Cricetidae (excepto *Oryzomys* y *Akodon*); Ako = *Akodon*; Cav = Caviidae; Oct = Octodontidae; Ech = Echimyidae + Abrocomidae.

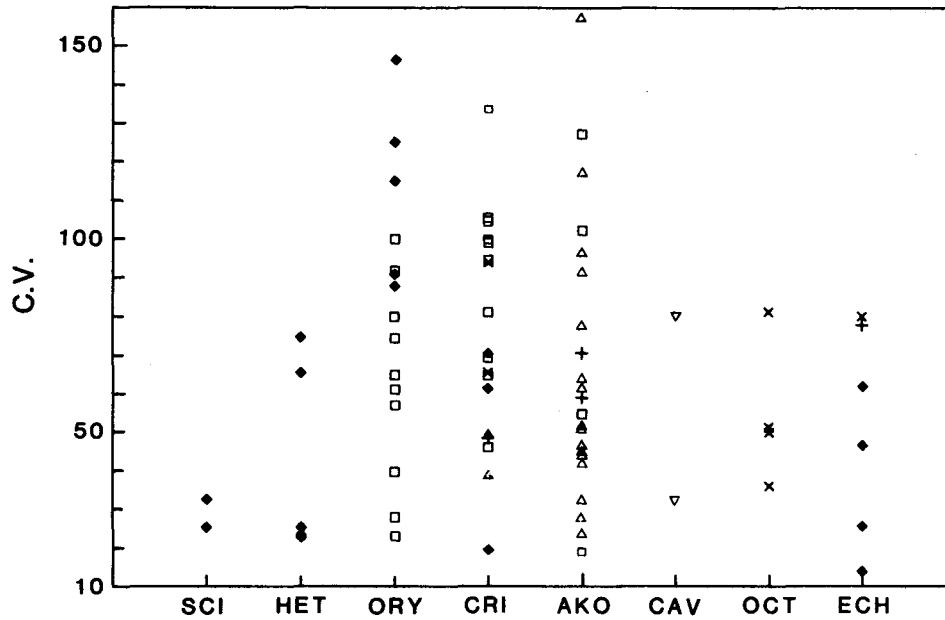


Fig. 3. The relation between coefficient of variation (CV) of reported density estimates and trophic category (following Eisenberg 1981) for neotropical rodent taxa. □ = Frugivore/omnivore; + = Frugivore/herbivore; ◆ = Frugivore/granivore; △ = Insectivore/omnivore; x = Herbivore/browser; ▽ = Herbivore/grazer. Taxon abbreviations as in Figure 2.

Relación entre el coeficiente de variación (CV) de los estimadores de densidad y la categoría trófica (de acuerdo a Eisenberg 1981) de roedores neotropicales. □ = Frugívoro/omnívoro; + = Frugívoro/herbívoros; ◆ = Frugívoro/granívoro; △ = Insectívoro/omnívoro; x = Herbívoro/ramoneador; ▽ = Herbívoro/pastoreador. Las abreviaciones para los roedores son las mismas que en la Figura 2.

TABLE 2

Comparison (one-way Analysis of Variance) of mean coefficients of variation (CV) for density estimates of Neotropical rodents with taxon, habitat, and trophic category. Sample size shown in parentheses. Abbreviations for trophic category as in Table 1. Means joined by lines are not significantly different (Student-Newman-Keuls Test).

Comparación (mediante análisis de varianza de una vía) de los coeficientes medios de variación (CV) para los estimadores de densidad de roedores neotropicales, de acuerdo al taxón, hábitat y categoría trófica. Los tamaños muestrales van entre paréntesis. Las abreviaciones para las categorías tróficas son las mismas que en la Tabla 1. Las medias conectadas por la misma línea no difieren significativamente entre sí (prueba de Student-Newman-Keuls).

TAXON	MEAN CV	HABITAT	MEAN CV	TROPHIC	MEAN CV
Cricetidae	73.8 (58)	Temperate forest	83.1 (17)	FR/OM	76.0 (24)
Caviidae	55.9 (2)	Tropical savanna	75.7 (10)	HB/GR	68.5 (3)
Octodontidae	54.5 (4)	Tropical humid forest	66.0 (12)	HB/BR	65.4 (7)
Echimyidae + <i>Abrocoma</i>	51.0 (6)	Temperate grassland	64.4 (25)	IN/OM	64.4 (16)
Heteromyidae	42.6 (5)	Tropical dry forest	57.5 (7)	FR/GR	62.4 (21)
Sciuridae	29.0 (2)	Tropical desert	50.7 (3)	FR/HB	59.9 (6)
		Tropical wet forest	20.1 (3)		
F = 2.16 (P < 0.07)		F = 2.25 (P < 0.05)		F = 0.50 (P < 0.78)	

Intra-taxon Comparisons

In addition to these general trends, examination of Table 1 and Figures 2 and 3 suggests considerable intra-taxon population variability. Some of this variation can be attributed to habitat and/or trophic differences; other cases are less clear cut.

The family Heteromyidae includes two Neotropical genera, *Liomys* and *Heteromys*. Both genera are frugivorous/granivorous, but the former is commonly associated with more xeric habitats (Fleming 1971, 1974, Genoways 1973) as compared to the latter (Rood & Test 1968, Fleming 1974, Handley 1976). Comparison of the CV's (Table 1, Figure 2) indicates that populations of *Liomys* from tropical dry forests and of *Heteromys* from mesic tropical forests are less variable than populations of *Heteromys* from more xeric tropical forests.

Proechimys is a common rodent in the forests of Central and northern South America, and typically contributes a large percentage of the non-volant small mammalian biomass (Gliwicz 1973, Eisenberg *et al.* 1979, Emmons 1982). Densities of *Proechimys* species vary between habitats (Gliwicz 1973, Eisenberg *et al.* 1979, Emmons 1982) as well as seasonally. Part of the difference in population variability observed (Table 1) might relate to sampling procedures. For example, more pronounced seasonal fluctuations were observed in Panamá (Fleming 1971) than in Venezuela (O'Connell 1981) or Trinidad (Everard & Tikasingh 1973). However, Fleming's year-long trapping began and ended in June (early wet season) when these animals are least likely to be trapped (Leigh & Smythe 1978), which would magnify apparent fluctuations.

The genus *Oryzomys* is widespread throughout the Neotropics and extends into the Nearctic. Rice rats have radiated into numerous habitats and several species are often sympatric (Fleming 1970). The highest mean densities of *Oryzomys* were observed in temperate grasslands and relatively aseasonal tropical forests (Table 1, Figure 2). In seasonal tropical forests, populations of *O. capito* were highest during the early to midwet season (Fleming 1971, O'Connell 1981). In contrast, population levels of *Oryzomys* from seasonal tropical savannahs were highest during the dry period (Valle *et al.* 1982). *Oryzomys*

populations from temperate grasslands and forests exhibit highest densities during autumn-winter months (Dalby 1975, Murúa *et al.*, in press). Clark (1980) suggested that populations of *Oryzomys* in tropical deserts and forests are more stable than those from temperate regions. Examination of Figure 2 indicates that this general trend is supported. Intra-specific differences (e.g., *O. capito*) in population variability are also related to habitat (Table 1).

The genus *Akodon* has radiated into a variety of habitats in the Neotropics. Seasonal fluctuations in populations of *Akodon* species have been observed in both temperate (Dalby 1975, Murúa & González 1985) and tropical (Davis 1945, O'Connell 1981) habitats. Examination of Figure 2 suggests no outstanding relationship between population variability and habitat. *Akodon* populations from temperate grasslands are somewhat less variable than those from tropical forests, but populations from temperate forests exhibit a tremendous range of variability. In the temperate habitats two or more *Akodon* species may be sympatric, and although densities differ, there is little relationship between density and variability. In some cases the numerical dominant exhibits greater variability than the less common species, but in others, the reverse is true (Table 1). Food habits vary between *Akodon* species (Figure 3) and within species (e.g., *A. longipilis*) from different areas (Meserve 1981, Pearson 1983). Again, there is no clear trend between population variability and trophic category. For example, although most populations of the insectivorous/omnivorous *Akodon* had lower CV's than other trophic categories, one population had the highest CV of any examined (Figure 3). However, it should be noted that in this case (*A. longipilis*; Murúa and Meserve, personal communication), the population had remained low ($\bar{x} = 1.8/\text{ha}$) throughout most of the study and increased substantially ($x = 17.5/\text{ha}$) for a two month period. Meserve (1981) suggested that sympatric *Akodon* species in Chile overlap in habitat use but exhibit dietary specialization. Glanz (1984) related dietary differences to morphological characteristics but suggested sympatric *Akodon* species exhibit microhabitat specialization as well. Removal experiments with these species indicate that interspecific competition plays a minimal role in affecting population

dynamics (Murua and Meserve, personal communication). Unraveling the factors influencing the population dynamics of this genus will depend on ongoing studies.

Neotropical rodents of a variety of taxa from different habitats periodically exhibit dramatic fluctuations in population size or "ratadas". These outbreaks have been recorded, for example, in *Akodon* and *Calomys* from temperate grasslands in Argentina (Crespo 1944, 1966, Dalby 1975); *Oryzomys* and *Phyllotis* from coastal Peru and Chile (Gilmore 1947, Pearson 1975, Pefaur *et al.* 1979); and *Zygodontomys* from tropical savannahs in Venezuela (O'Connell 1982). Although the factors underlying these outbreaks vary between habitats, they are typically associated with local climatic or resource conditions (e.g., increased rainfall, effects of el Niño, seed set of bamboo, annual patterns of flooding). The close correlation of these outbreaks with local conditions and their irregular timing suggest that they are irruptions rather than cyclic fluctuations.

Assessment of the temporal dynamics of rodent populations must include consideration of numerous factors (e.g., Jaksić *et al.* 1981, Asher & Thomas 1985) and for Neotropical populations will depend on a database of long-term studies from many habitats. I have limited my treatment only to very general comparisons: body mass, taxon, broad habitat association, and simplified trophic category. These comparisons suggest that population variability is inversely related to body mass and that habitat exerts an influence on population variability in these rodents. French *et al.* (1975) reviewed the demographic patterns of small mammals on a worldwide basis and concluded that taxonomic groups were characterized by different degrees of population stability. For example, populations of Murids and microtines were classified as high density (66-118/ha) and unstable, whereas populations of cricetines, Heteromyids, and Scurids were considered low density (7-15/ha) and stable (French *et al.* 1975). Their review included few Neotropical rodent species, reflecting the paucity of data at that time. My results indicate that whereas Neotropical Scurids and Heteromyids generally fit the above conclusion, generalizations become more difficult when comparisons are focused within the cricetines. Populations of some

cricetines are found at relatively low and stable densities whereas others (even conspecifics in different habitats) are characterized by greater and highly variable densities. This variability is attributable to the responsiveness of local populations to microhabitat differences and the effects of seasonal and yearly climatic patterns on resource abundance and distribution.

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