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# Chapter 2

# Taxonomy, Distribution, and Natural History of the Genus *Heteromys* (Rodentia: Heteromyidae) in Central and Eastern Venezuela, with the Description of a New Species from the Cordillera de la Costa

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## ABSTRACT

*Heteromys anomalus* is widely distributed along the Caribbean coast of South America and had been considered the only spiny pocket mouse present in Venezuela for several decades. Recent taxonomic studies in western Venezuela, however, have documented the presence of *H. australis* from the Cordillera de Mérida and described *H. oasicus* from the Península de Paraguaná. Here, we revise the genus *Heteromys* in central and eastern Venezuela as well as in Trinidad and Tobago. Morphological comparisons with samples of *H. anomalus* from throughout its known range in Venezuela and with representatives of all other recognized species of the genus indicate the existence of a species new to science, which we describe as *Heteromys catopterius* (the Overlook Spiny Pocket Mouse). This species ranges from 350 to 2425 m in elevation in the Cordillera de la Costa in northern Venezuela, with the vast majority of records above ca. 700 m. In central and eastern Venezuela, *H. anomalus* is found in the surrounding lowlands and lower slopes of the Cordillera. Externally, *H. catopterius* is darker than *H. anomalus* and lacks the distinctly rounded ears of that species. The new species averages larger than *H. anomalus* for most external and cranial measurements. Cranially, the two species have differences in proportion; the skulls of *H. catopterius* are proportionately wider (less elongated) than those of *H. anomalus*, with a relatively wider interorbital constriction, wider interparietal, and more inflated braincase. *Heteromys catopterius* occurs in wet montane forests (especially cloud forests) in four highland areas of the Cordillera de la Costa: the main Aragua-Carabobo chain, the El Ávila massif, the Serranía del Interior, and the Macizo Oriental. Presumably, the warm, dry lowlands of the Depresión de Unare represent a barrier for the species, separating populations in the Macizo Oriental from the more westerly populations. Large areas of the known ranges of both *H. catopterius* and *H. anomalus* are protected in the Venezuelan network of protected areas.

## INTRODUCTION

The rodent family Heteromyidae is endemic to North and South America and includes three subfamilies: Dipodomyinae (kangaroo rats and kangaroo mice), Perognathinae (pocket mice, both silky and coarse haired), and Heteromyinae (spiny pocket mice; Wilson and Cole, 2000; Patton, 2005). Heteromyines represent a well-defined monophyletic group distinct from the two other living subfamilies (Hafner, 1981; Hafner and Hafner, 1983; Wahlert, 1991; Hafner et al., 2007; see also Ryan, 1989: 94–98; Brylski, 1990). Two extant genera, *Heteromys* and *Liomys*, are recognized in the Heteromyinae

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and can be distinguished from each other by a number of morphological characters (Williams et al., 1993; Anderson, 2003b; Patton, 2005; Anderson et al., 2006). Although phylogenetic analyses based on sequences of mitochondrial DNA indicate that *Liomys* is likely paraphyletic (and no synapomorphies for it are known), *Heteromys* has been recovered as monophyletic in studies using both morphological and genetic data (including several synapomorphies; Rogers and Vance, 2005; Anderson et al., 2006; Hafner et al., 2007). Some authors have suggested that all heteromyines should be placed in the genus *Heteromys* to avoid recognition of a paraphyletic *Liomys* (Hafner et al., 2007). However, we continue to recognize *Liomys* (sensu Williams et al., 1993; Patton, 2005) until conclusive studies with multiple independent data sources (e.g., unlinked nuclear markers) can be completed, allowing for a comprehensive reevaluation of the generic-level taxonomy of the subfamily (see Anderson et al., 2006: 1227)[3]. Species of *Liomys* inhabit deciduous forests and other semiarid tropical and subtropical habitats from southern Texas and northern Mexico to Panama (Genoways, 1973; Morales and Engstrom, 1989; Rogers and Engstrom, 1992; Williams et al., 1993), and species of *Heteromys* occur in relatively wet (typically evergreen) forests from southern Mexico to western Ecuador (Williams et al., 1993; Anderson, 1999, 2003b; Anderson and Jarrín-V., 2002). Whereas most species of heteromyids inhabit western North America, *Heteromys* is the only genus of the family to have colonized South America.

Present taxonomy recognizes nine species of *Heteromys*, including three that have been described recently (Williams et al., 1993; Anderson and Jarrín-V., 2002; Anderson, 2003b; Patton, 2005; Anderson and Timm, 2006). *Heteromys desmarestianus*, *H. gaumeri*, *H. nelsoni*, *H. nubicolens*, and *H. oresterus* are restricted to Central America and Mexico (but see Anderson, 1999, for one marginal locality of *H. desmarestianus* in extreme northwestern Colombia). In addition, two species are known to have extensive distributions in northwestern South America, and three others have restricted distributions there. For several decades, the widespread *H. anomalus* and *H. australis* were the only two species recognized for the main body of South America, with a marginal distribution indicated for *H. desmarestianus* (Cabrera, 1961; Honacki et al., 1982; Patton, 1993). *Heteromys australis* inhabits very mesic evergreen forests in the lowlands of the Chocó in northwestern Ecuador, western Colombia, and eastern Panama, as well as throughout much of the Colombian Andes up to ca. 2500 m in elevation (Anderson, 1999). An apparently disjunct population also exists in the Río Uribante drainage of the Cordillera de Mérida in western Venezuela (Anderson and Soriano, 1999; Anderson et al., 2002a). In contrast, *H. anomalus* inhabits both deciduous and evergreen tropical forests in northern South America, typically from near sea level up to ca. 1500–1600 m. It is distributed along the Caribbean coast of Colombia and Venezuela (including the Isla de Margarita) and in Trinidad and Tobago (Musso-Q., 1962; Anderson, 1999, 2003b; Anderson and Soriano, 1999), but not in Panama (Anderson, 1999; contra Rogers, 1990; Méndez, 1993;

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[3] All recent phylogenetic studies of the Heteromyinae have recovered three monophyletic groups: (1) *Heteromys*; (2) *Liomys adspersus* and *L. salvini*; and (3) *L. irroratus*, *L. pictus*, and *L. spectabilis* (Rogers and Vance, 2005; Anderson et al., 2006; Hafner et al., 2007). The relationships among the three clades could not be resolved using morphological and allozymic data (Anderson et al., 2006). Analyses of DNA sequences from linked mitochondrial genes indicated that the *L. adspersus–L. salvini* clade occupies a basal position in the subfamily, sister to the remaining two clades (Rogers and Vance, 2005; Hafner et al., 2007). If this topology is corroborated by analyses of other independent datasets (e.g., sequences of multiple unlinked nuclear markers), generic-level taxonomy should be modified to reflect reconstructed evolutionary relationships in the group. Furthermore, given the substantial morphological, ecological, and genetic distinctiveness of the three clades (Genoways, 1973; Anderson et al., 2006), recognition of three genera would be warranted regardless of the relationships among the three clades (i.e., even if *Liomys*, as currently conceived, is not paraphyletic). An available name exists for the basal *adspersus–salvini* clade: *Schaeferia* (first described as a subgenus of *Liomys*, with type species *H. salvini*; von Lehmann and Schaefer, 1979: 232). Elevation of *Schaeferia* to full generic status, restriction of *Liomys* (with type species *H. alleni*, currently considered a synonym of *L. irroratus*) to members of the *irroratus–pictus–spectabilis* clade, and retention of current usage of *Heteromys* (with type species *Mus anomalus*) would provide valid genera for each of the monophyletic groups, acknowledge the substantial morphological and ecological distinctiveness of the three clades, and maximally preserve nomenclatural stability in the subfamily.

Williams et al., 1993; Nowak, 1999). The species is also known from parts of the dry upper Río Magdalena Valley in Colombia (Hernández-Camacho, 1956; Anderson, 1999, 2003b). In addition to these long-recognized taxa with large distributions, *H. teleus* was described recently from central-western Ecuador, where it inhabits highly seasonal evergreen forests (Anderson and Jarrín-V., 2002). Subsequently, *H. oasicus* was described from small areas of mesic vegetation on the Península de Paraguaná in northwestern Venezuela (Anderson, 2003b). Finally, a species of the *Heteromys desmarestianus* complex (provisionally referred to as *H. d. crassirostris*) has been confirmed for one locality in the Serranía del Darién in extreme northwestern Colombia, west of the Río Atrato–Río San Juan lowlands (= Bolívar Geosyncline; Hershkovitz, 1972); the species' distribution continues to the west in Panamá (Anderson, 1999; Anderson et al., 2006).

Here, we evaluate the taxonomic status of populations of *Heteromys* from central and eastern Venezuela, as well as Trinidad and Tobago. A previous study revised the genus in western Venezuela but noted the presence of an unrecognized species to the east and the need for taxonomic study of populations from that region (Anderson, 2003b: 24). In doing so, the current work completes the revision of the genus in the easternmost portion of its distribution (Venezuela and Trinidad and Tobago). Future work should reevaluate populations in central Colombia that may be specifically distinct from *H. australis* (Anderson, 1999: 620).

## MATERIALS AND METHODS

### Museum Specimens

We examined 1349 specimens of *Heteromys* from the principal study area of central and eastern Venezuela, as well as Trinidad and Tobago (appendix 1). Central and eastern Venezuela is here considered as the area east of the Río Yaracuy and the Río Cojedes (and its continuations, the Río Portuguesa and Río Apure). These rivers define the Depresión de Yaracuy (SAGCN, 1995; ≈ Depresión de Lara sensu Soriano et al., 1999), a lowland region that separates the Cordillera de Mérida (and Sierra de Aroa) from the Cordillera de la Costa (fig. 1). Material reported here from the principal study area (appendix 1) includes the overwhelming majority of specimens of *Heteromys* from that region available in museums in the United States and Venezuela, as well as critical historical material in the United Kingdom.

We also examined selected specimens from other regions (appendix 2). For statistical analyses, we took advantage of the several large series of *Heteromys* available from localities throughout northern Venezuela. We also examined representative samples of all currently recognized species of *Heteromys*, including all holotypes and lectotypes representing nominal taxa currently referred to the genus, with the exception of *H. desmarestianus psakastus*; in lieu of that holotype, we examined eight paratypes. Apparently, no holotype exists for *H. thompsonii*, a name that Lesson (1827) clearly used to refer to the spiny pocket mouse from Trinidad named by Thompson (1815) as *Mus anomalus*, now referred to as *H. anomalus*. We also report two specimens from western Venezuela that were not included in Anderson (2003b).

We examined external and cranial morphological characters, making comparisons among specimens of approximately the same age. Cranial nomenclature follows Wahlert (1985), Anderson and Timm (2006), and Anderson et al. (2006); see also Anderson (1999, 2003b) and Anderson and Jarrín-V. (2002). Specimens were assigned to the age classes of Rogers and Schmidly (1982) based on patterns of tooth eruption, toothwear, and molt. Age classes 1–3 represent juveniles and subadults, and classes 4–6 are progressively older adults. Age classes do not constitute a continuous variable (such as absolute age), but rather are categories roughly corresponding to relative age within population samples (Voss et al., 1990).

Localities and specimens examined from central and eastern Venezuela and from Trinidad and Tobago are detailed in the Gazetteer (appendix 1), and other specimens examined are listed separately (appendix 2). Specimens examined are housed in the

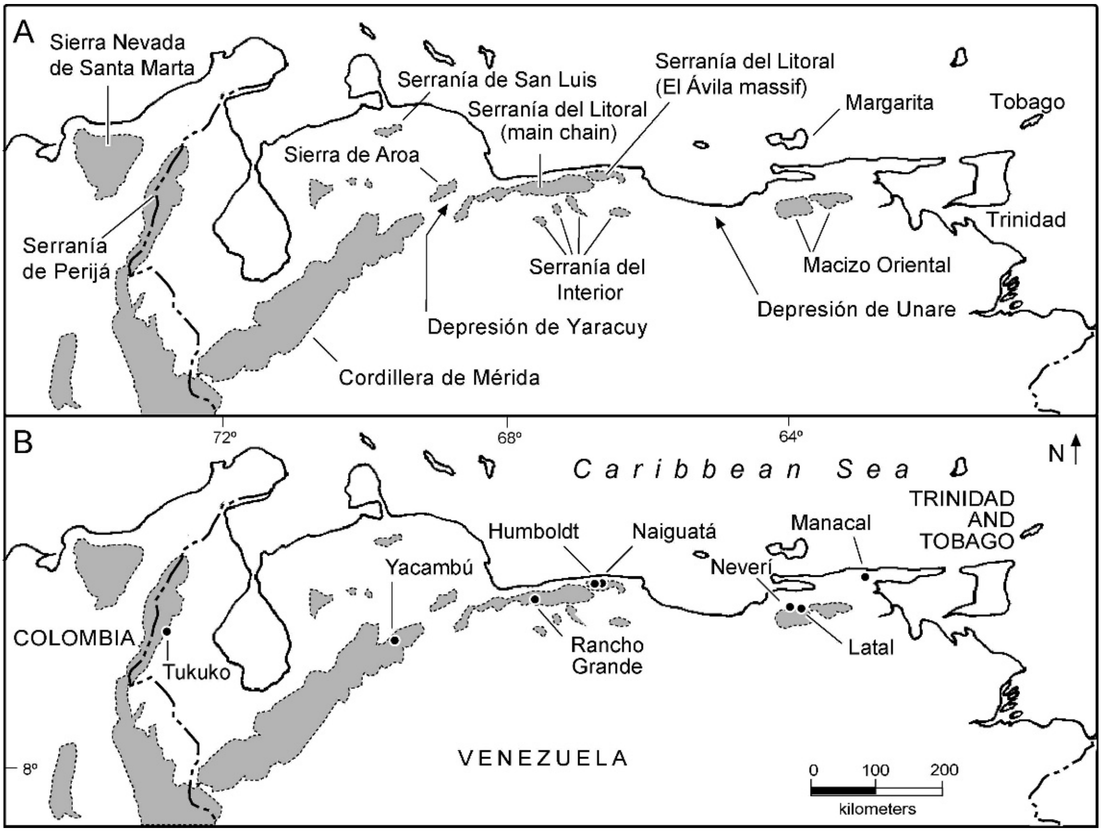

Fig. 1. Map of north-central South America. Gray shading approximates regions above 1000 m in elevation. **A** (upper): Major geographic features mentioned in the text. **B** (lower): Location of primary geographic samples of *Heteromys* used in this study. See Materials and Methods and appendices 1 and 2 for complete provenience and museum catalog numbers.

following museum collections (where applicable, abbreviations follow Lew and Ochoa, 1993; Bisbal-E. and Sánchez-H., 1997; and Hafner et al., 1997). An asterisk (*) denotes museums with material from central and eastern Venezuela or from Trinidad and Tobago.

| | |
|---|---|
| AMNH | American Museum of Natural History, New York* |
| ANSP | Academy of Natural Sciences of Philadelphia, Philadelphia |
| BM(NH) | Natural History Museum, London [formerly British Museum (Natural History)]* |
| CM | Carnegie Museum of Natural History, Pittsburgh* |
| CUVC | Cornell University Vertebrate Collections, Ithaca* |
| CVULA | Colección de Vertebrados de la Universidad de los Andes, Mérida |
| EBRG | Museo de la Estación Biológica de Rancho Grande, Maracay* |
| FMNH | Field Museum, Chicago [formerly Field Museum of Natural History]* |
| ICN | Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá |
| KU | University of Kansas Natural History Museum, Lawrence* |
| MBUCV | Museo de Biología de la Universidad Central de Venezuela, Caracas* |
| MCNUSB | Museo de Ciencias Naturales de la Universidad Simón Bolívar, Caracas* |

| | |
|---|---|
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge* |
| MHNLS | Museo de Historia Natural La Salle, Caracas* |
| MIZA | Museo del Instituto de Zoología Agrícola de la Facultad de Agronomía de la Universidad Central de Venezuela, Maracay* |
| MNCR | Museo Nacional de Costa Rica, San José |
| MVZ | Museum of Vertebrate Zoology, University of California, Berkeley |
| TCWC | Texas Cooperative Wildlife Collection, Texas A&M University, College Station* |
| TTU | Museum of Texas Tech University, Lubbock* |
| UF | Florida Museum of Natural History, University of Florida, Gainesville* |
| UMMZ | University of Michigan Museum of Zoology, Ann Arbor* |
| USNM | United States National Museum of Natural History, Washington, DC* |
| UV | Universidad del Valle, Cali* |
| UWZM | University of Wisconsin Zoological Museum, Madison* |

## MEASUREMENTS

Standard cranial measurements for *Heteromys* (fig. 2) follow Anderson and Jarrín-V. (2002) and were taken to the nearest 0.01 mm with digital calipers on selected specimens (see below). External measurements and mass were copied from specimen tags and, when necessary, from primary field notes or museum catalogs. We calculated head-and-body length by subtracting tail length from total length.

*Occipitonasal length* (ONL): greatest distance from anteriormost projection of nasal bones to posteriormost portion of occipital bone.

*Zygomatic breadth* (ZB): greatest width across zygomatic arches at right angle to longitudinal axis of cranium.

*Rostral length* (RL): greatest distance from notch lateral to lacrimal bone to anteriormost projection of nasal bone on same side of cranium.

*Nasal length* (NL): greatest distance from anteriormost projection of one nasal bone to its posteriormost projection (not necessarily at medial suture between nasals).

*Least interorbital constriction* (IOC): least width across interorbital constriction at right angle to longitudinal axis of cranium.

*Squamosal breadth* (SB): width across squamosals anterior to external auditory meatus at right angle to longitudinal axis of cranium.

*Maxillary toothrow length* (MTR): distance from anterior lip of alveolus of premolar to posterior lip of alveolus of third molar.

*Interparietal width* (IW): greatest transverse width measured from lateralmost projections of interparietal bone at right angle to longitudinal axis of cranium.

*Interparietal length* (IL): greatest distance from anteriormost projection of interparietal bone to posteriormost border of interparietal bone, always taken along medial line of cranium even when notch present in posterior border.

*Parietal breadth* (PB): greatest width across parietal crests at right angle to longitudinal axis of cranium.

*Skull depth* (SD): greatest distance from dorsalmost point of braincase to horizontal plane passing through ventral borders of maxillary cheek teeth and ventral borders of occipital condyles (taken by placing skull on glass microscope slide with upper incisors rested over edge of slide, and then subtracting thickness of slide).

## STATISTICS

GENERAL PROTOCOLS: We conducted quantitative analyses to characterize external and cranial morphology and examine nongeographic, geographic, and interspecific variation in Venezuelan *Heteromys*. Statistical analyses were performed with Minitab (2003; version 14.1). To test for any departure from normality in our quantitative data, we conducted Ryan-Joiner tests on the relevant residuals (see below). To correct for multiple unplanned comparisons, we determined significance within families of tests (e.g., within a series of *t*-tests, each comparing the mean between two samples for one of several variables) using Holm's (1979) modification of the Bonferroni procedure. In all other cases, we compared probabilities to an $\alpha = 0.05$. Past studies indicated that sexual dimorphism was insubstantial in the few cases where it was

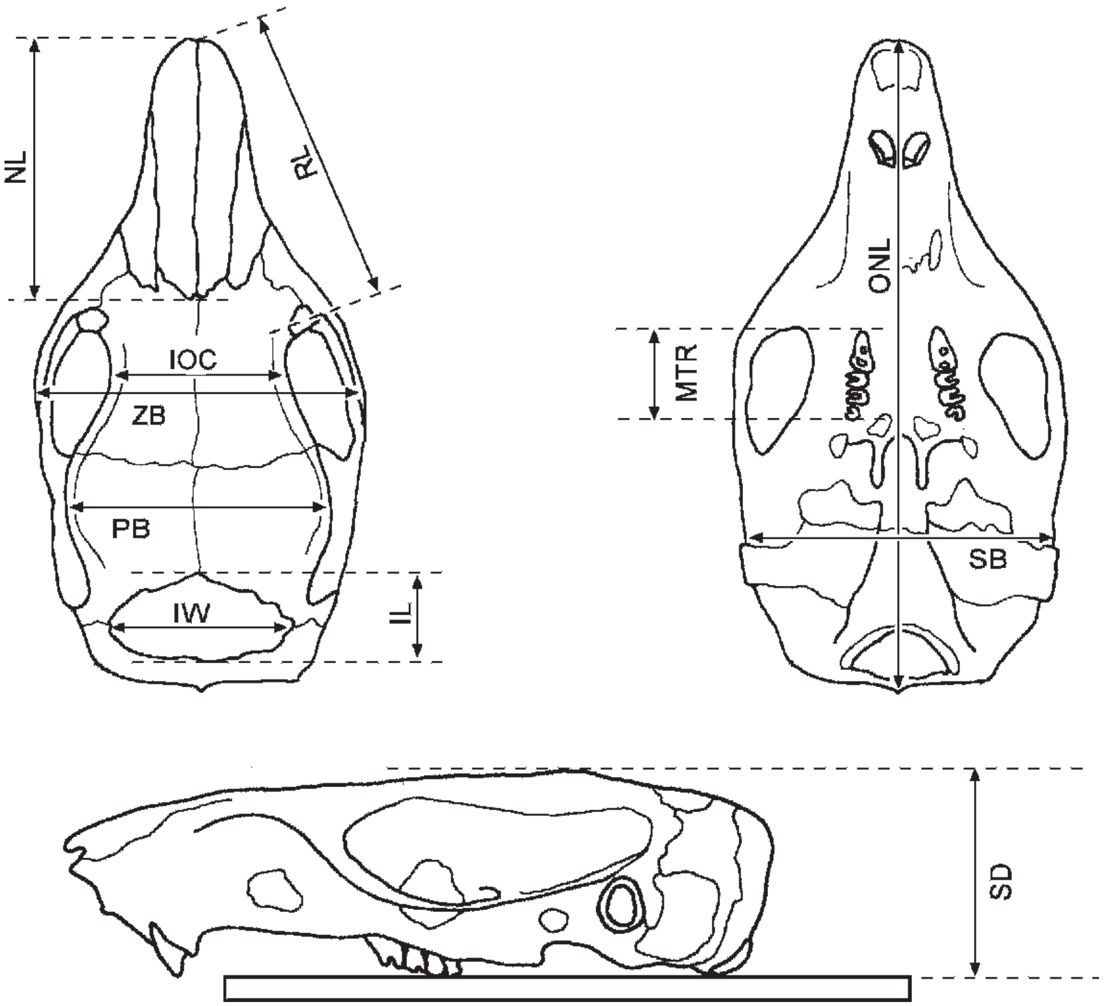

Fig. 2. Dorsal, ventral, and lateral views of a cranium of *Heteromys* showing the methods for taking measurements. Abbreviations and measurements are defined in Materials and Methods.

detected in species of *Heteromys* (Engstrom et al., 1987; Best, 1993). Nevertheless, we test for sexual dimorphism (see Nongeographic and Interspecific Variation); based on the results (see below), males and females were pooled in all other analyses. Species assignments for quantitative analyses were based on our qualitative morphological examinations.

In addition to univariate descriptive and inferential statistics (see below), we conducted principal components analysis (PCA) to examine geographic and interspecific variation from a multivariate perspective. Each PCA was performed on the covariance matrix of log-transformed cranial measurements following Jolicoeur (1963); natural logarithms ($\log_e$ or ln) were used here. PCA is a multivariate-ordination technique that extracts axes of maximum dispersion among observations (here, specimens) without regard to the group (e.g., geographic sample) to which they belong. Each resultant axis (principal component) is characterized by an eigenvector with coefficients that indicate the relationship of each variable (here, cranial measurements) to that multivariate axis. We interpreted the principal components by examination of both coefficients (elements) of the unit eigenvector and of loadings, which are Pearson product–moment correlation coefficients between specimen scores on each axis and the log-transformed variables. We only interpreted principal components with clearly distinct eigenvalues (by inspection).

GEOGRAPHIC AND INTERSPECIFIC VARIATION (PRIMARY GEOGRAPHIC SAMPLES): We conducted a series of quantitative analyses using eight primary geographic samples of adult *Heteromys* in age class 4 (the most abundant adult age class) from selected sites across northern Venezuela (fig. 1; appendices 1 and 2). The six samples of *H. anomalus* spanned northern Venezuela (*Tukuko*, Estado Zulia, locality 97 of Anderson, 2003b; *Yacambú*, Estado Lara, locality 58 of Anderson, 2003b; *Naiguatá*, Estado Vargas, locality 120; *Neverí*, Estado Sucre, locality 111; *Latal*, Estado Sucre, locality 113; and *Manacal*, Estado Sucre, locality 100). We also included two highland samples from the Cordillera de la Costa representing the putative new highland species (*Rancho Grande*, Estado Aragua, locality 137; and *Humboldt*, Estado Miranda/Estado Vargas, locality 156). These geographic samples were chosen for their relatively large sample sizes and geographic dispersion. Each contains specimens from a single latitude–longitude combination (i.e., specimens with different textual locality descriptions were pooled if they held the same geographic coordinates; appendices 1 and 2; see also Anderson, 2003b). Although specimens of both *H. anomalus* and the new species are known from Naiguatá (localities 120 and 160), only individuals matching the morphological diagnosis of *H. anomalus* are included here in this primary geographic sample (locality 120).

Using specimens from these primary geographic samples, we conducted both univariate and multivariate analyses. First, we calculated descriptive statistics for specimens in age class 4 from each of the eight primary geographic samples, as well as for the two putative species (based on the same individuals but grouped by species rather than by geographic sample). We calculated these statistics for external measurements, mass, cranial measurements, and one derived variable (head-and-body length; table 1, appendix 3). Using these same individuals, we then conducted a series of two-tailed *t*-tests comparing means of the two species for the same measurements and derived variable (these constituted a family for correction for multiple unplanned comparisons). For each variable, we used residuals from these two samples (i.e., after taking species into account) for tests of normality, again correcting for multiple unplanned comparisons. In addition, to test for proportional differences between the species, we examined three ratios of external and cranial variables (tail length/head-and-body length; IOC/ONL; and IW/ONL). Because ratios seldom are distributed normally (Sokal and Rohlf, 1995), we conducted nonparametric tests here (two-tailed Mann-Whitney *U*-test). Finally, to examine the multivariate structure of the data and determine how much of the variation among specimens of the same age class (age class 4) corresponds to geographic and interspecific variation, the 11 cranial measurements for specimens from these samples were submitted to PCA.

NONGEOGRAPHIC AND INTERSPECIFIC VARIATION (SITE OF SYMPATRY): To assess nongeographic variation (including tests for sexual dimorphism) and examine interspecific differences between the species further, we took advantage of one site of sympatry where large samples of both species are available. For Los Canales de Naiguatá (localities 120 and 160), many specimens of each species exist in museum collections; these specimens correspond to all age classes, but age classes 1–4 are especially well represented. Hence, this site provides an opportunity to test for sexual dimorphism (and age-related variation) and examine interspecific variation (across age classes) without the complication of geographic variation in either species. To assess and characterize any differences between the sexes in each species, we performed a two-way General Linear Model (GLM; unbalanced ANOVA) for each cranial measurement, with age class and sex as the two fixed factors (and testing for an interaction term of age class by sex). Here, we used only age classes 1–4, because very few specimens were available in age classes 5 and 6. These GLMs for each species test for differences among the age classes (controlling for sex), differences between the sexes (controlling for age class), and any possible interactions between age class and sex. This series of GLMs for age class and sex made up a family for correction for multiple unplanned comparisons. Similar to the analyses for the principal geographic samples, we used residuals from these samples (after taking into account both age class and sex) for each variable to test for departures from normality (again correcting for multiple unplanned comparisons).

We assessed interspecific differences at Los Canales de Naiguatá in several ways. First, we calculated descriptive statistics of each species for specimens from this site in each of the age classes 1–4, respectively. We calculated these statistics for all 11 cranial measurements (appendix 4). Second, we performed a second series of two-way GLMs for each cranial measurement, with age class and species as fixed factors, and testing for an interaction term of age class by species. As in the earlier GLMs, we used only age classes 1–4. These analyses test for differences among the age classes (controlling for species), differences between the species (controlling for age class), and any possible interactions between age class and species. This series of GLMs for age class and species formed a family for correction for multiple unplanned comparisons. As above, residuals from these samples (here, after taking into account both age class and species) for each variable were used to test for departures from normality (once again correcting for multiple unplanned comparisons). Third, we performed a PCA using cranial measurements for all available specimens from Los Canales de Naiguatá with intact skulls (age classes 1–6). Because of high levels of variation in interparietal width and interparietal length, those measurements were excluded from this analysis, which was conducted with the remaining nine cranial measurements.

GEOGRAPHIC VARIATION IN THE HIGHLAND SPECIES: We also performed analyses aimed at assessing geographic variation within the highland species. First, we conducted a PCA on cranial measurements of all specimens of the putative new species in age class 4 with intact skulls (i.e., from all known localities of the species; appendix 1). As above, interparietal width and interparietal length were excluded from this analysis, which was conducted with the remaining nine cranial measurements. We also conducted two-tailed *t*-tests between the primary geographic samples of *Rancho Grande* and *Humboldt* (see above) to detect any difference in mean for each external and cranial measurement (and the derived variable head-and-body length) for specimens in age class 4 (these composed a family for correction for multiple unplanned comparisons). As before, we conducted a Mann-Whitney *U*-test to assess differences between the populations for the tail length/head-and-body length ratio.

## SYSTEMATICS

### A NEW SPECIES OF *HETEROMYS* FROM THE CORDILLERA DE LA COSTA IN VENEZUELA

Our analyses indicate that two species of *Heteromys* exist in central and eastern Venezuela. In this region, *Heteromys anomalus* is widely distributed in fairly mesic lowland areas up to intermediate elevations in the Cordillera de la Costa. The other species is restricted to intermediate and high elevations of the Cordillera de la Costa. It differs externally and cranially from *H. anomalus* and shows differences from all other recognized species of the genus. As no available name exists for this species, we describe it as:

### ***Heteromys catopterius***, new species

Overlook Spiny Pocket Mouse
Figures 3, 6, 7, 8, and 9

HOLOTYPE: USNM 517536, adult male; skin and skull in excellent condition (fig. 3). Collected on 20 March 1960 from Venezuela: Aragua: Rancho Grande, near Biological Station, 13 km NW Maracay [10°21′N, 67°40′W] at 3576 ft [1090 m] elevation by Charles O. Handley, Jr., and Daniel I. Rhymer; original number COH, Jr. 7778.

PARATYPES: We designate as paratypes the following 31 specimens (adults in age class 4; skins and skulls in good condition) from the type locality, and housed in eight museum collections (appendix 1): EBRG 190, 4317; KU 120294, 120295; MCNUSB I-423, 424,

TABLE 1

**Descriptive Statistics and Results of Comparisons of Adults in Age Class 4 of *Heteromys anomalus* and *H. catopterius* in Venezuela for External Variables, Mass, and Cranial Measurements**

Mean ± standard error, sample size, and observed range (minimum–maximum) are given for each species. Probabilities associated with differences in mean between the two species in two-tailed *t*-tests (or in median for the Mann-Whitney *U*-test, for the tail length/head-and-body length ratio) are indicated as follows: * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; n.s. = $P > 0.05$. To correct for multiple unplanned comparisons, we determined significance within this family of tests using Holm's (1979) modification of the Bonferroni procedure; here, this altered the statistical conclusion only for hind foot length, which was no longer significant after correction for multiple comparisons. Note that for all significant comparisons, *H. catopterius* averages larger than *H. anomalus*. Linear measurements are in millimeters, mass is in grams, and the ratio is multiplied by 100 to yield a percent.

| | *H. anomalus* | *H. catopterius* |
|---|---|---|
| Total length** | 289 ± 2, 64<br>(257–327) | 298 ± 2, 37<br>(270–324) |
| Head-and-body length (n.s.) | 129 ± 1, 65<br>(115–151) | 132 ± 2, 38<br>(113–149) |
| Tail length** | 160 ± 1, 64<br>(134–180) | 166 ± 2, 35<br>(147–192) |
| Tail length/head-and-body length ratio, × 100 (%; n.s.) | 124 ± 1, 64<br>(108–146) | 127 ± 2, 35<br>(100–152) |
| Hind foot length* (but see table header) | 35 ± 0, 65<br>(31–38) | 36 ± 0, 37<br>(32–39) |
| Ear length (n.s.) | 18 ± 0, 41<br>(15–22) | 19 ± 0, 37<br>(14–22) |
| Mass (grams)*** | 61 ± 2, 40<br>(42–100) | 82 ± 4, 19<br>(59–119) |
| Occipitonasal length*** | 35.37 ± 0.17, 83<br>(31.06–39.02) | 36.64 ± 0.14, 46<br>(34.74–38.66) |
| Zygomatic breadth*** | 16.21 ± 0.07, 83<br>(14.42–17.90) | 16.76 ± 0.10, 46<br>(15.52–18.17) |
| Rostral length*** | 15.66 ± 0.09, 83<br>(13.60–17.60) | 16.29 ± 0.08, 46<br>(14.98–17.57) |
| Nasal length*** | 14.24 ± 0.08, 83<br>(11.93–16.10) | 14.69 ± 0.09, 46<br>(13.45–15.93) |
| Least interorbital constriction*** | 8.38 ± 0.04, 83<br>(7.66–9.78) | 9.13 ± 0.06, 46<br>(8.13–10.13) |
| Squamosal breadth*** | 15.01 ± 0.05, 83<br>(14.09–16.00) | 15.48 ± 0.07, 46<br>(14.67–16.56) |
| Maxillary toothrow length*** | 5.38 ± 0.03, 83<br>(4.67–6.05) | 5.56 ± 0.03, 46<br>(5.14–5.94) |
| Interparietal width*** | 8.74 ± 0.07, 83<br>(7.06–10.30) | 9.42 ± 0.12, 46<br>(7.72–11.01) |
| Interparietal length (n.s.) | 5.04 ± 0.05, 83<br>(4.03–5.83) | 4.93 ± 0.07, 46<br>(3.95–6.07) |
| Parietal breadth*** | 12.54 ± 0.04, 83<br>(11.67–13.94) | 13.10 ± 0.07, 46<br>(11.91–14.00) |
| Skull depth*** | 11.01 ± 0.03, 83<br>(10.35–11.65) | 11.42 ± 0.05, 46<br>(10.70–12.07) |

581, 1357; MIZA 20-024, 20-028, 20-049, 20-130; UF 13709; UMMZ 110768, 110771; USNM 517533, 517534, 517538–517541, 517543, 517545, 517546, 517558, 517563, 517564, 517566, 517567, 517569; UWZM S.31418.

ETYMOLOGY: The adjective *catopterius* derives from the Greek *katoptêrios* (from *kata*, "down" and *opter*, "eyewitness, scout"; Brown, 1956: 279, 693). *Katoptêrios* was applied to a "height that commands a view" (Liddell and Scott, 1961) in classical texts

Fig. 3. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype of *Heteromys catopterius* (USNM 517536), an adult male in age class 4. See text and appendix 1 for full provenience.

(e.g., by the geographer Strabo) and is used here as an adjective to mean "commanding a view" or "having a spectacular or wide/panoramic view" (M. Knight, in litt.). We apply this name to the new species in reference to its presence on the rugged and steep-sided Cordillera de la Costa along the littoral of northern Venezuela, from which magnificent views derive, especially of the Caribbean coast. Suitable common names include Overlook Spiny Pocket Mouse (English); and Ratón de Abazones del Mirador, Ratón Bolsero del Mirador, and Ratón Mochilero del Mirador (Spanish).

DISTRIBUTION: Known only from the Cordillera de la Costa of north-central and northeastern Venezuela (figs. 1, 4, 5). The species has been documented from all four major subranges of the Cordillera de la Costa: the main Aragua-Carabobo chain and the El Ávila massif (which together form the Serranía del Litoral), the Serranía del Interior, and the Macizo Oriental. The known elevational range of the species is 350–2425 m, but the vast majority of known records of the species correspond to highland sites above ca. 700 m. See also Sympatry and Zones of Contact with *Heteromys anomalus*, below.

DIAGNOSIS: A species of spiny pocket mouse with adults showing the following combination of characters (figs. 3, 6, 7, 8, 9): p4 (lower permanent premolar) with three lophids; P4 (permanent upper premolar) with straight, moderately long fold in anterior margin of posterior loph; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone; parietomastoid suture parallel to parietal crest throughout its length; rostrum long and wide (only slightly to moderately tapered anteriorly), without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital constriction wide; braincase wide and moderately inflated; interparietal wide; skull average for genus (ONL 34.74–38.66 mm in adult specimens of age class 4; table 1, appendix 3); dorsal coloration dark slate gray or black and only moderately grizzled with thin ochraceous hairs intermixed among spines; distinctive patch of dark coloration present on dorsal and external surfaces of forearms, continuous with dark coloration of flanks; ears dark gray to black and medium in size; orange band on flanks absent; plantar surface of hind feet naked.

DESCRIPTION: Dorsal pelage (fig. 6) dark slate gray or black (sharply contrasting with soft, white pelage of venter) and moderately grizzled with thin ochraceous hairs intermixed among spines, typically moderately spiny, but soft in some populations; distinctive patch of dark coloration present on dorsal and external surfaces of forearms, continuous with dark coloration of flanks; ventral and internal surfaces of forearms white; orange band on flanks absent; ears dark gray to blackish and medium in size; tail strongly bicolored, and slightly to moderately longer than head-and-body length (table 1, appendix 3); hind feet average for genus (table 1, appendix 3), with plantar surface naked; skull (figs. 3, 7, 8, 9) average for genus (ONL 34.74–38.66 mm in adult specimens of age class 4; table 1, appendix 3); rostrum long and wide (only slightly to moderately tapered anteriorly), without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital region moderately inflated; interorbital constriction wide; braincase wide and moderately inflated; parietal and temporal crests weakly to moderately developed; interparietal variable (moderately wide to very wide), sometimes with distinctive lateral and anterior points; incisive foramina usually short, wide, and anteriorly tapering; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; parapterygoid fossa deep; postalar fissure large and distinctly rounded anteriorly; optic foramen especially small, with posterior margin formed by strong bar of bone; parietomastoid suture parallel to parietal crest throughout its length; anterodorsal lobe of periotic capsule variable in size, sometimes causing notable undulation in posterior margin of squamosal (see Geographic Variation; see schematic drawing in Anderson,

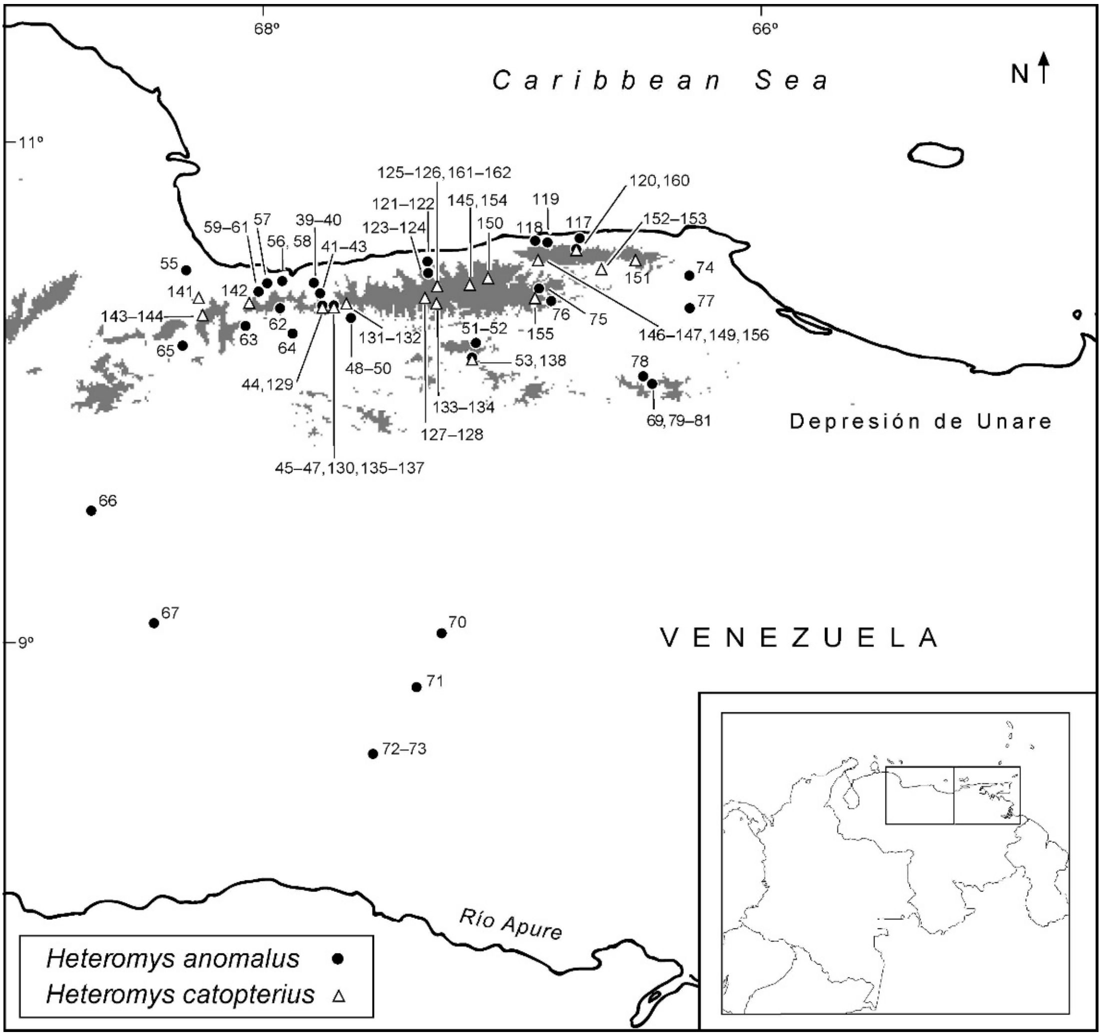

Fig. 4. Maps showing collection localities for *Heteromys* in central and eastern Venezuela and in Trinidad and Tobago. Locality numbers correspond to data given in the Gazetteer (appendix 1). *Heteromys anomalus* continues its distribution to the west (not shown) in northwestern Venezuela, northern Colombia, and the Río Magdalena Valley in central Colombia (see Anderson, 2003b). Only georeferenced localities are plotted here with symbols. Gray shading denotes regions higher than 1000 m in elevation.

1999: 619); jugular foramen (anterolateral to occipital condyle) medium in size; dental formula: (incisors 1/1, canines 0/0, premolars 1/1; molars 3/3) × 2 = total 20; molars variable in size (notably large and robust in some populations but typical for genus in others); lateral borders of lophs of molars smooth, not pointed; lophs of M2 subequal in width; P4 (permanent upper premolar) with straight, moderately long fold in anterior margin of posterior loph, and with smoothly curved posterior border; p4 (lower permanent premolar) with 3 lophids; m3 not reduced, approximately same width as p4.

MEASUREMENTS OF THE HOLOTYPE (mm): total length 321, tail length 186, hind foot length 37, ear length 21, ONL 36.98, ZB 17.52, RL 16.40, NL 15.18, IOC 9.27, SB 16.14, MTR 5.88, IW 10.47, IL 5.08, PB 13.48, SD 11.78. Mass not available.

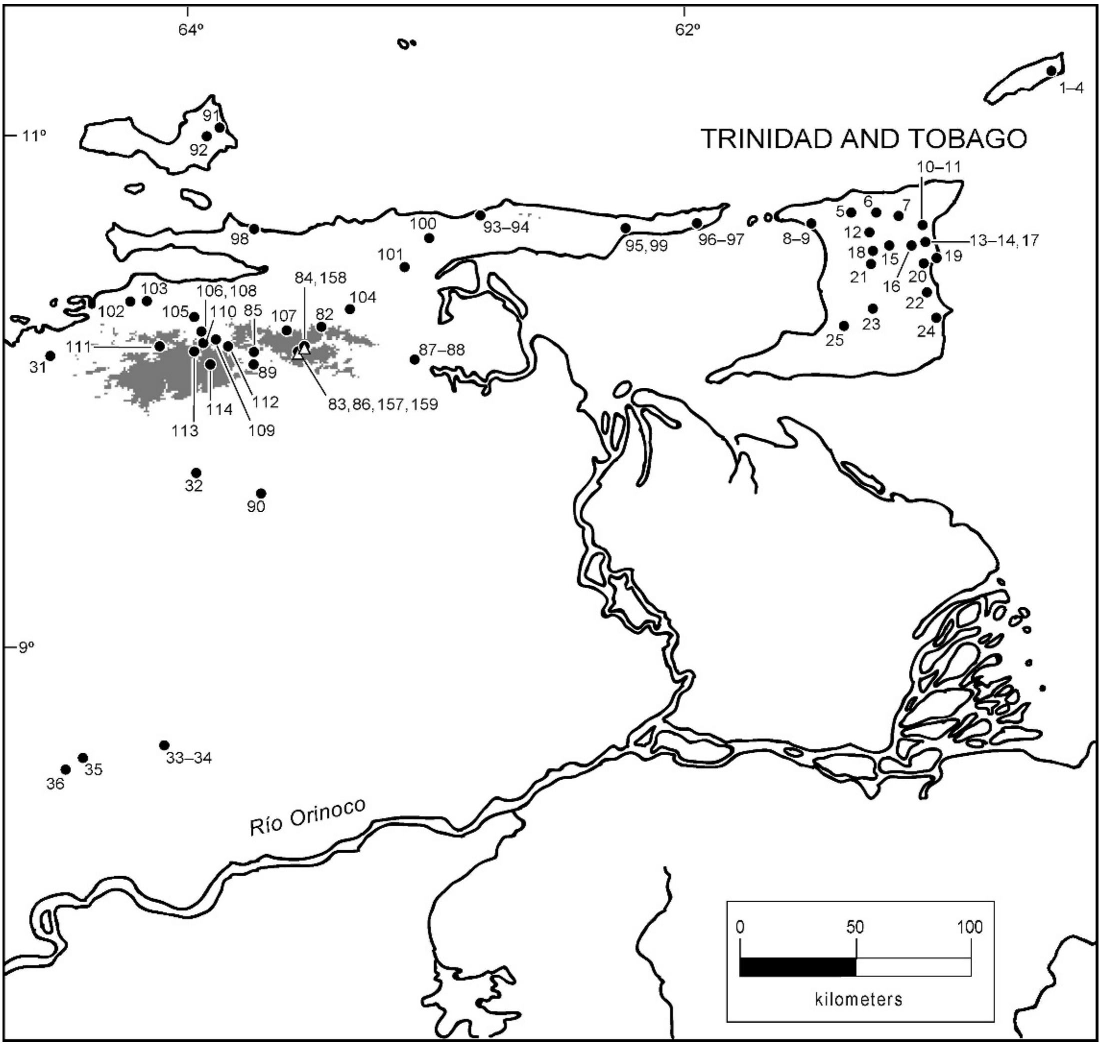

Fig. 4. *(Continued)*

KARYOLOGY: Schmid et al. (1992) reported karyotypic information for three individuals of the species now known as *Heteromys catopterius* from the northern slope of the Cordillera de la Costa along the Maracay–Ocumare de la Costa highway at 940 m in Estado Aragua (locality 130), very near the type locality of Rancho Grande (MIZA 20-391, 20-392, and 20-394; appendix 1). These individuals possessed a standard karyotype with a diploid number of 2n = 60 and a fundamental number of FN = 72. Note, however, that those authors included the four arms of the sex chromosomes in the count for the fundamental number; under standard counting protocols, this karyotype would have a FN = 68 (M. Aguilera, in litt.). Various banding and staining techniques were conducted as well; the Y chromosome shows exceptional quinacrine-positive heterochromatin, indicative of a preponderance of AT-rich sequences (Schmid et al., 1992). Although the standard karyotype of *H. catopterius* is the same as that of *H. anomalus* (see account of that species below), some species of the genus with identical standard karyotypes have been shown to be very distinct based on DNA sequences and morphology (i.e., *H. nubicolens* and nearby populations of *H. desmarestianus*; Anderson

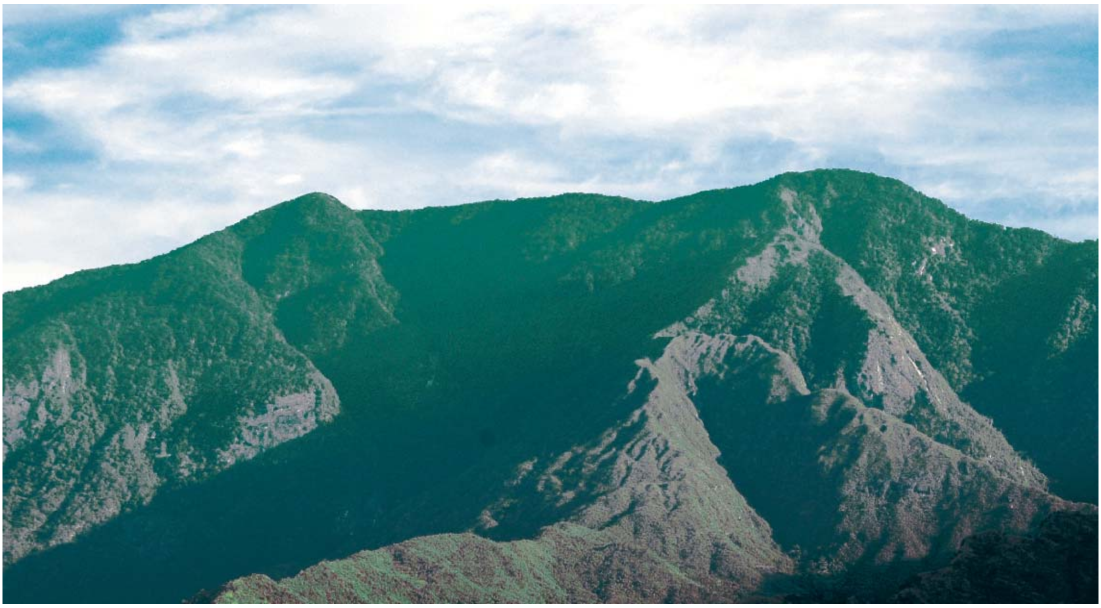

Fig. 5. Landscape on the southern slopes of the Serranía del Litoral of the Cordillera de la Costa in Estado Carabobo and Estado Aragua. Here, *Heteromys catopterius* inhabits areas above ca. 1000 m (principally cloud forests), and *H. anomalus* occurs in other forested areas at lower elevations. Rancho Grande (locality 137), the type locality of *H. catopterius*, lies near the western peak. Photographed by Eliécer E. Gutiérrez in January 2008, from the northern outskirts of the city of Maracay.

Fig. 6. Dorsal external morphology of adult male specimens in age class 4 of two species of *Heteromys* from the Rancho Grande/El Limón region in Estado Aragua, Venezuela, illustrating interspecific variation based on samples in close geographic proximity: *Heteromys catopterius* (top), Rancho Grande, near Biological Station, 13 km NW Maracay, 3576 ft [1090 m] (USNM 517536; holotype of *Heteromys catopterius*; locality 137) and *H. anomalus* (bottom), Rancho Grande [region], El Limón, 4 km NW Maracay, 524 m (USNM 517544; locality 50).

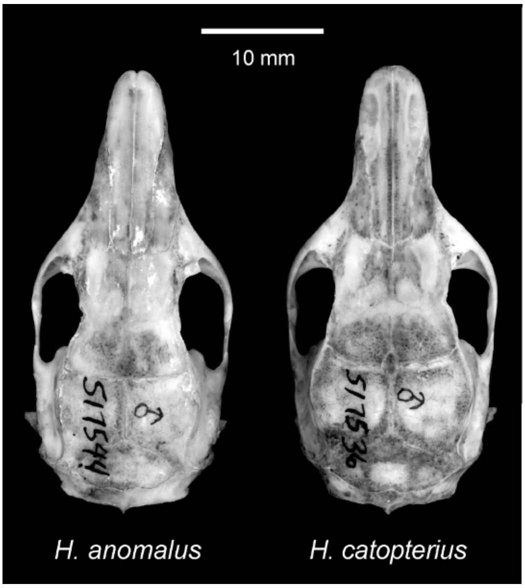

Fig. 7. Dorsal views of the crania of adult male specimens in age class 4 of two species of *Heteromys* from the Rancho Grande/El Limón region in Estado Aragua, Venezuela, illustrating interspecific variation based on samples in close geographic proximity: *Heteromys anomalus*, Rancho Grande [region], El Limón, 4 km NW Maracay, 524 m (left, USNM 517544; locality 50) and *H. catopterius*, Rancho Grande, near Biological Station, 13 km NW Maracay, 3576 ft [1090 m] (right, USNM 517536; holotype of *Heteromys catopterius*; locality 137).

et al., 2006; Anderson and Timm, 2006; Anderson and Jansa, 2007); future banding studies are necessary to compare the cytogenetics of *H. catopterius* and *H. anomalus* in more detail.

COMPARISONS: Externally, the dark slate-gray dorsal pelage (only moderately grizzled with ochraceous hairs; fig. 6) of *Heteromys catopterius* differentiates it from most currently recognized species of the genus. Three types of dorsal pelage are present in the genus (pale brown, strongly grizzled; dark brown, moderately grizzled; and dark slate gray, nearly uniform to moderately grizzled). In contrast to the new species, *Heteromys gaumeri*, *H. oasicus*, and most populations of *H. anomalus* have pale brown dorsal pelage that is strongly grizzled with thin ochraceous hairs intermixed among the spines (Anderson, 2003b). In addition, specimens of *H. gaumeri* possess an orange band on the flanks that is absent in *H. catopterius*. The dwarf species *H. oasicus* is much smaller than *H. catopterius* (total length 227–250 mm for adults in age class 4; Anderson 2003b). *Heteromys gaumeri* is restricted geographically to Belize, Guatemala, and the Península de Yucatán in Mexico (Williams et al., 1993). *Heteromys oasicus* inhabits only the Península de Paraguaná in northwestern Venezuela, to the northwest of known records of *H. catopterius* (Anderson, 2003b). *Heteromys anomalus* inhabits much of northern South America and comes into geographic contact with *H. catopterius* in several areas; because the pelage of *H. anomalus* is atypically dark in a few portions of its range (i.e., similar to that of *H. catopterius*), detailed comparisons are necessary to ensure proper identification (see below). The pelage of *H. catopterius* also differs from the dark-brown pelage of *H. nubicolens* and members of the *H. desmarestianus* species complex, which occur in Mexico and Central America far from the known distribution of *H. catopterius* (Anderson and Timm, 2006; *H. d. crassirostris* also has a marginal distribution in South America in extreme northwestern Colombia; Anderson, 1999).

*Heteromys catopterius* shares dark slate-gray pelage with several other species of the genus (*H. australis*, *H. nelsoni*, *H. oresterus*, and *H. teleus*). Both *H. nelsoni* and *H. oresterus* display extremely soft dorsal pelage, in contrast to the pelage of *H. catopterius*, which is spiny in most populations (all known populations except those from the Macizo Oriental). They are distributed in restricted highland regions of extreme southeastern Mexico and southwestern Guatemala (*H. nelsoni*) and the Cordillera de Talamanca in Costa Rica (*H. oresterus*; Rogers and Rogers, 1992; Williams et al., 1993; Reid, 1997), respectively. *Heteromys teleus* and *H. australis* are extremely similar to *H. catopterius* externally, although their pelage tends to be even darker than that of *H. catopterius*. Like the new species, they also inhabit South America but are not known to come into geographic contact with it. *Heteromys teleus* is endemic to western Ecuador, and the distribution of *H. australis* extends from

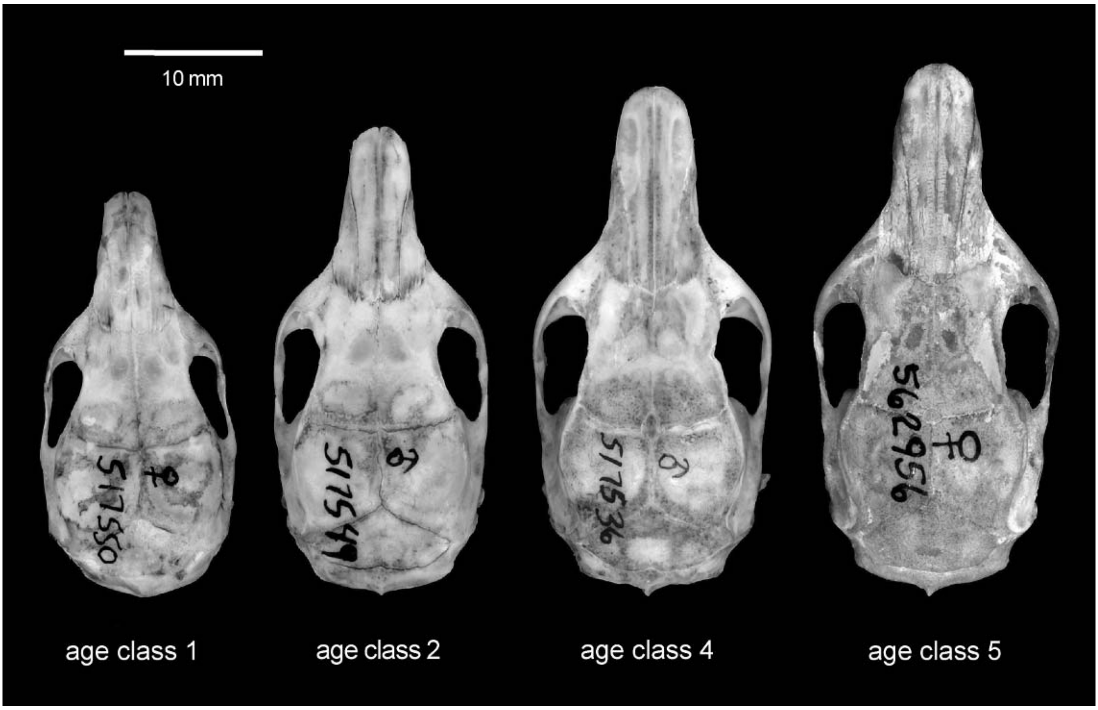

Fig. 8. Dorsal views of the crania of specimens of *Heteromys catopterius* from the Rancho Grande region (Estado Aragua) in several age classes, showing growth-related differences in size and shape. All specimens derive from localities 131 and 137, only ca. 2 km distant from each other at elevations of 3576–4900 ft [1090–1494 m] (USNM 517550, age class 1; USNM 517549, age class 2; USNM 517536, age class 4; USNM 562956, age class 5). Such marked differences among age classes are typical of species of the genus (see Anderson and Timm, 2006: 14) and complicate identification and characterization of nongeographic, geographic, and interspecific variation. See appendix 1 for full provenience.

northwestern Ecuador and extreme eastern Panama through much of Colombia to western Venezuela; Anderson, 1999, 2003b; Anderson and Jarrín-V., 2002). Cranial characters are necessary to distinguish them from *H. catopterius*.

Cranial characters serve to separate *Heteromys catopterius* from all other species of the genus (figs. 3, 7, 8, 9). *Heteromys catopterius* differs from *H. gaumeri* by the narrow postalar fissure and deeply concave (collapsed) anterior termination of the premaxillary of *H. gaumeri*. Additionally, the form of the premaxillary in *H. gaumeri* creates a distinct step in the lateral border of the rostrum in dorsal view, a character lacking in the new species (Anderson et al., 2006). *Heteromys catopterius* contrasts with the Central American and Mexican species *H. desmarestianus*, *H. nelsoni*, *H. nubicolens*, and *H. oresterus* by its especially small optic foramen and straight, only moderately long fold in the anterior margin of the posterior loph of P4. Consistent, but more subtle, differences exist in comparison with other South American species. *Heteromys oasicus* is much smaller than the new species and has a much less-developed rostrum (Anderson, 2003b). In comparison with *H. catopterius*, the braincase of *H. australis* is even more inflated and the rostrum less developed. *Heteromys teleus* is very similar to the new species cranially but has wider (bowed) zygomatic arches and an uninflated braincase. These three species inhabit areas of South America to the west of the known distribution of *H. catopterius*. Cranial differences also separate *H. catopterius* from *H. anomalus* (see detailed comparisons below).

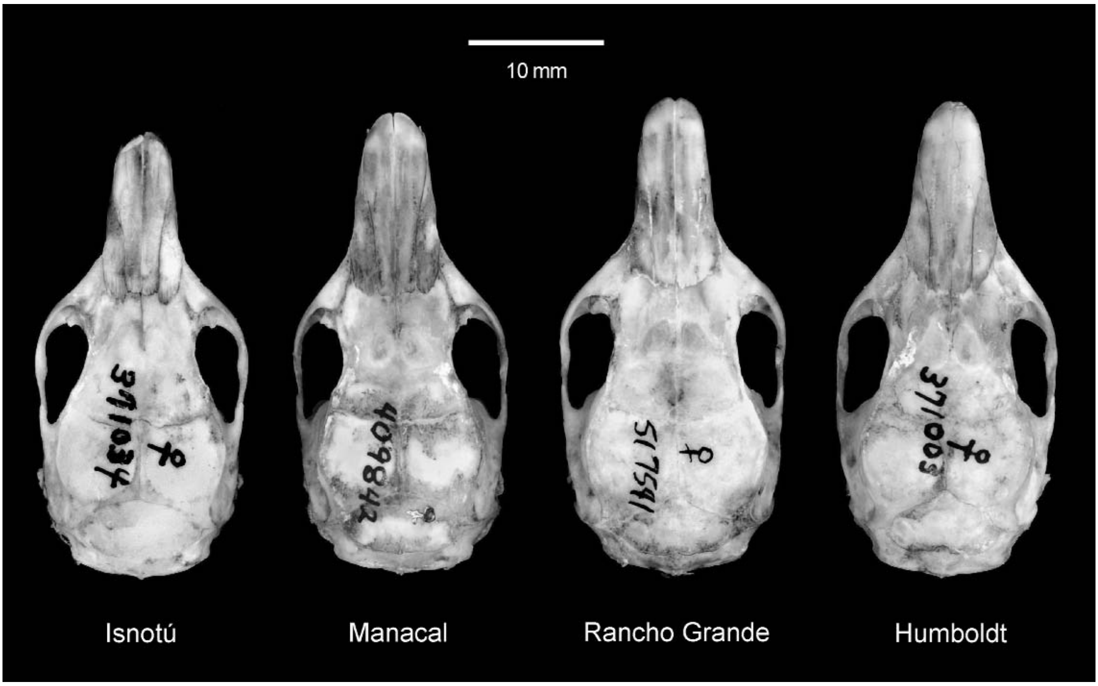

Fig. 9. Dorsal views of the crania of adult female specimens in age class 4 of *Heteromys anomalus* (two crania on left) and *H. catopterius* (two crania on right) from Venezuela, showing interspecific and geographic variation: *H. anomalus* from 10 km WNW Valera, Isnotú, 930 m (Estado Trujillo; locality 82 in Anderson, 2003b) and 5 km S and 25 km E Carúpano, Manacal, 185 m (Estado Sucre; locality 100) and *H. catopterius* from Rancho Grande, near Biological Station, 13 km NW Maracay, 3576 ft [1090 m] (Estado Aragua; locality 137) and Hotel Humboldt, 9.4 km N Caracas, 2181 m (Estado Miranda/Estado Vargas; locality 156). See appendices 1 and 2 for full provenience.

External differences exist between *Heteromys catopterius* and *H. anomalus*. Externally, most populations of *H. anomalus* have a pale brown dorsal pelage that is strongly grizzled with thin ochraceous hairs, in stark contrast to the dark slate-gray dorsal pelage (only moderately grizzled with ochraceous hairs) of *H. catopterius*. In addition, *H. catopterius* possesses a distinctive patch of gray or black on the forearm; the homologous patch is present in *H. anomalus* as well, but it is typically paler and brownish. However, some populations of *H. anomalus* from mesic areas (e.g., some regions of Estados Lara, Monagas, Sucre, and Zulia in Venezuela, and the island of Tobago in Trinidad and Tobago) exhibit a much darker dorsal pelage, very similar to that of *H. catopterius* in general aspect and in the coloration of the patch on the forearm. Notably, however, *H. anomalus* has distinctively rounded ears throughout its range, in contrast to *H. catopterius* and all other species of the genus (which have moderately pointed ears). Additionally, *H. catopterius* has much longer, darker mystacial vibrissae than *H. anomalus* (fig. 6).

Cranial differences in size and shape also distinguish *Heteromys catopterius* from *H. anomalus*. Overall, the skull of the new species is larger than that of *H. anomalus* and relatively wider (less elongated). Regarding proportional differences, *H. catopterius* generally shows a more inflated braincase, a relatively wider interorbital constriction, and a relatively wider interparietal. In addition, it tends to possess wider (often short and anteriorly tapering) incisive foramina (the incisive foramina of *H. anomalus* vary geographically but tend to be longer, thinner, and more parallel sided than those of *H. catopterius*).

The analyses of nongeographic variation in cranial measurements at Los Canales de Naiguatá documented strong age-related differences but no sexual dimorphism. The GLMs of individuals of *H. anomalus* in age classes 1–4 showed highly significant age-related differences for all variables but maxillary toothrow length, interparietal width, and interparietal length ($P < 0.002$ for significant comparisions; $P = 0.152$ for IW; $P = 0.312$ for IL; $P = 0.003$ for MTR, not significant after correction for multiple comparisons). Sex was not significant for any variable ($P = 0.023$ for ZB; $P = 0.045$ for IOC, neither significant after correction for multiple comparisons; $P = 0.080$–$0.779$ for other nonsignificant comparisons). No interaction term was significant ($P = 0.064$–$0.451$). Furthermore, no variable showed a departure from normaility ($P > 0.058$). Results for *H. catopterius* were similar. For this species, age class was significant for all variables but interparietal width, interparietal length, and parietal breadth ($P < 0.002$ for significant comparisions; $P = 0.107$ for IL; $P = 0.007$ for IW; $P = 0.006$ for PB, neither of the latter two significant after correction for multiple comparisons). Sex was never significant ($P = 0.486$–$0.992$), nor was any interaction term ($P = 0.042$ for PB, not significant after correction for multiple comparisons; $P = 0.376$–$0.996$ for other nonsignificant comparisons). As in the tests for *H. anomalus*, no variable showed a departure from normaility ($P = 0.040$ for SB; $P = 0.030$ for MTR, neither significant after correction for multiple comparisons; $P > 0.079$ for other nonsignificant comparisons).

Quantitative comparisons documented differences in size and shape between *Heteromys catopterius* and *H. anomalus*. Even though the two species overlapped for mass and all external and cranial variables (for specimens in age class 4 from the primary geographic samples), means were significantly different for some external variables, mass, and most cranial variables (but no variable showed a departure from normality; $P = 0.040$ for mass; $P = 0.030$ for IOC, neither significant after correction for multiple comparisons; $P > 0.100$ for other nonsignificant comparisons). For external variables and mass, only total length, tail length, and mass were significant ($P < 0.005$ for significant comparisons; $P = 0.147$ for head-and-body length; $P = 0.171$ for ear length; $P = 0.025$ for hind foot length, not significant after correction for multiple comparisons; table 1). The corresponding test for a difference in median for the tail length/head-and-body length ratio was not significant ($P = 0.090$). All cranial measurements except interparietal length showed significant differences in mean between the two species ($P < 0.001$ for significant comparisons; $P = 0.200$ for IL; table 1). For all significant comparisons, *H. catopterius* averaged larger than *H. anomalus* (see also figs. 7, 9). Regarding differences in cranial shape, *H. catopterius* showed a relatively wider interorbital constriction and relatively wider interparietal (IOC/ONL ratio, $P < 0.001$; IW/ONL ratio, $P = 0.007$).

Quantitative analyses document similar differences between *Heteromys catopterius* and *H. anomalus* at a site of sympatry. At Los Canales de Naiguatá, both species and age class were important factors (but no variable showed a departure from normality; $P = 0.041$ for MTR, not significant after correction for multiple comparisons; $P > 0.086$ for other nonsignificant comparisons). These GLMs for age classes 1–4 documented that the species were significantly different for all cranial measurements but interparietal width and interparietal length ($P < 0.001$ for significant comparisions; $P = 0.210$ for IL; $P = 0.035$ for IW, not significant after correction for multiple comparisons). Age class was significant for all measurements but IW ($P < 0.004$ for significant comparisons; $P = 0.005$ for IW, not significant after correction for multiple comparisons), but no interaction term was significant ($P = 0.393$–$0.991$). *Heteromys catopterius* averaged larger than *H. anomalus* for all measurements that were significantly different.

Multivariate analyses also supported the morphological distinctiveness of *Heteromys catopterius* from *H. anomalus*. In a plot of scores on the first two principal components of the PCA undertaken on specimens in age class 4 from the primary geographic samples, substantial but incomplete overlap occurred between specimens of the two species (fig. 10). The coefficients and loadings of PC1 were all of the same sign, indicating that

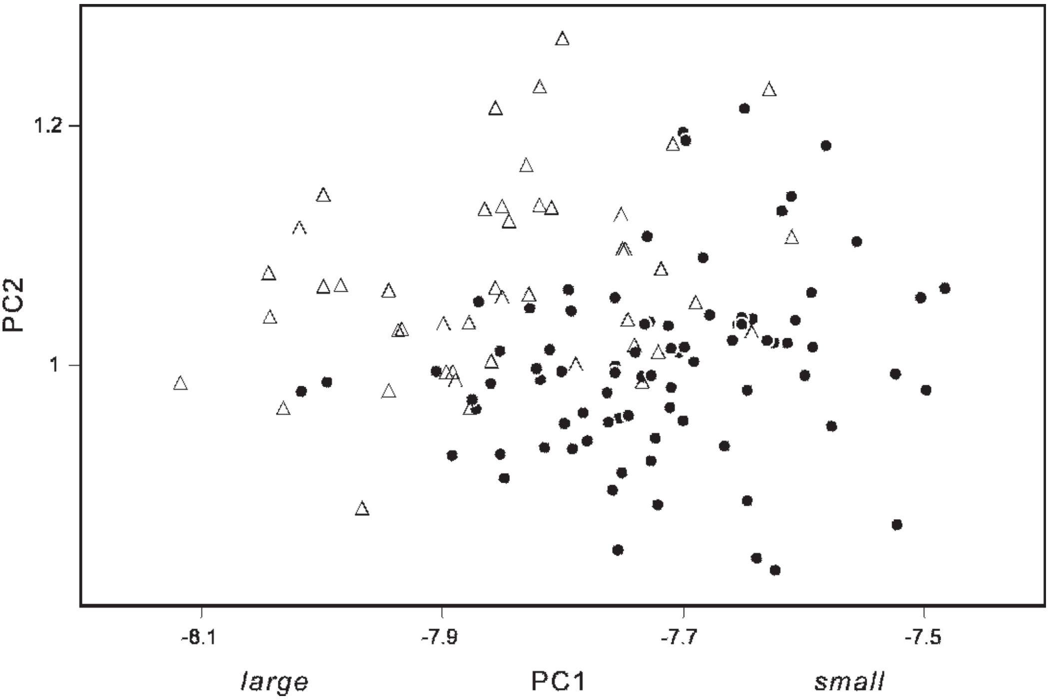

Fig. 10. Plot of specimen scores on the first two axes of the principal components analysis of 11 cranial measurements of adult specimens of *Heteromys* in age class 4 from the eight primary geographic samples across northern Venezuela. Specimens of *H. anomalus* are marked by circles, and individuals of *H. catopterius* are denoted by triangles. PC1 is a size axis (with larger specimens appearing toward the left side of the plot), and PC2 represents a shape difference (see text and table 2).

TABLE 2

**Results of Principal Components Analysis of Adult Specimens in Age Class 4 of *Heteromys anomalus* and *H. catopterius* from Primary Geographic Samples across Northern Venezuela (see fig. 10)**

Elements of the unit eigenvector and loadings are presented for the first three principal components. Eleven cranial measurements were transformed to their natural logarithms (ln) before computation of the covariance matrix and extraction of components. Eigenvalues (multiplied by 100) and the percentage of variation among specimens explained are given for each axis.

| | Unit eigenvector | | | Loadings | | |
|---|---|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC1 | PC2 | PC3 |
| ln-Occipitonasal length | −0.263 | 0.079 | −0.263 | −0.815 | 0.161 | −0.443 |
| ln-Zygomatic breadth | −0.294 | 0.070 | −0.118 | −0.872 | 0.136 | −0.190 |
| ln-Rostral length | −0.274 | 0.162 | −0.351 | −0.725 | 0.283 | −0.506 |
| ln-Nasal length | −0.296 | 0.129 | −0.371 | −0.733 | 0.211 | −0.500 |
| ln-Least interorbital constriction | −0.384 | 0.270 | −0.020 | −0.817 | 0.378 | −0.023 |
| ln-Squamosal breadth | −0.205 | 0.066 | −0.015 | −0.820 | 0.174 | −0.033 |
| ln-Maxillary toothrow length | −0.221 | 0.097 | −0.175 | −0.585 | 0.169 | −0.252 |
| ln-Interparietal width | −0.491 | 0.021 | 0.762 | −0.752 | 0.021 | 0.636 |
| ln-Interparietal length | −0.322 | −0.922 | −0.150 | −0.465 | −0.876 | −0.118 |
| ln-Parietal breadth | −0.229 | 0.022 | 0.145 | −0.763 | 0.048 | 0.262 |
| ln-Skull depth | −0.216 | 0.085 | 0.002 | −0.830 | 0.215 | 0.004 |
| Eigenvalue (× 100) | 1.645 | 0.711 | 0.487 | | | |
| % variation explained | 49.7 | 21.5 | 14.7 | | | |

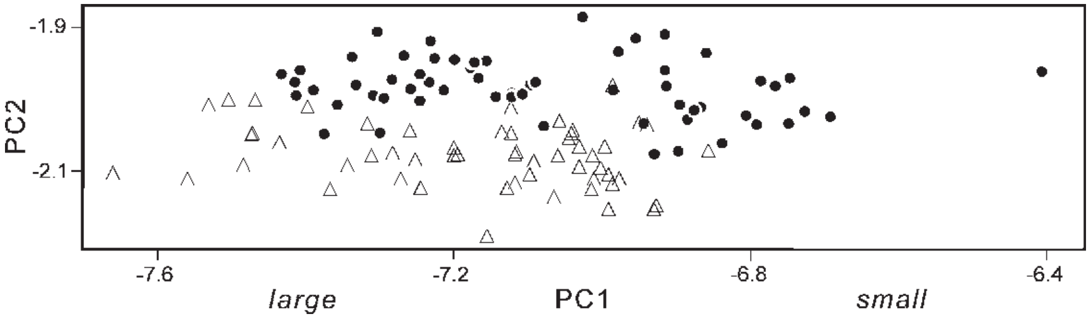

Fig. 11. Plot of specimen scores on the first two axes of a principal components analysis of nine cranial measurements of specimens of *Heteromys anomalus* (circles) and *H. catopterius* (triangles) in all age classes from Los Canales de Naiguatá (localities 120 and 160). PC1 represents a size axis (with larger specimens appearing toward the left side of the plot), and PC2 portrays a difference in shape (see text and table 3).

it represented a size axis (with larger specimens having lower scores, because the signs of the coefficients were all negative; table 2). In contrast, PC2 represented a shape axis (because most coefficients were positive, but that of interparietal length was negative; table 2).

Multivariate differences between the two species were much clearer when considering specimens from only one site. At Los Canales de Naiguatá, only very limited overlap between *Heteromys catopterius* and *H. anomalus* existed in a plot of scores on the first two principal components of the PCA undertaken on specimens in all age classes (using all cranial measurements but interparietal width and interparietal length; fig. 11). As above, the coefficients and loadings of PC1 were all of the same sign, indicating that it represented a size axis (again with larger specimens showing lower scores, since the signs of all the coefficients were negative; table 3). Here, PC2 again constituted a shape axis (because some coefficients were positive and others negative; table 3), but the axis was very different than the one for the PCA for the primary geographic samples. At Los Canales de Naiguatá, PC2 represented a contrast between occipitonasal length, rostral length, and nasal length vs. zygomatic breadth, least interorbital constriction, squamosal breadth, maxillary toothrow length, parietal breadth, and skull depth. Specimens with larger values for the former three measurements relative to their values for the latter ones showed larger (less negative) scores on this axis. This analysis indicated strong shape differences between the two species, with *H. anomalus* more elongated than the relatively wider *H. catopterius*. Accordingly, a bivariate plot of least interorbital constriction vs. nasal length (fig. 12) showed a clear difference in shape between the two species: with very little overlap, specimens of *H. anomalus* exhibited a longer nasal length relative to least interorbital constriction (and individuals of *H. catopterius* showed a wider least interorbital constriction relative to nasal length).

In sum, the quantitative analyses indicate that adult *Heteromys catopterius* were larger in overall body size than those of *H. anomalus* and differed in cranial proportions (figs. 7, 9, 10, 11, 12). Almost all measurements averaged larger for *H. catopterius*, table 1, appendices 3 and 4). Furthermore, *H. catopterius* showed a relatively wider, less-elongated skull (with relatively wider interorbital constriction and interparietal). These differences in shape were also evident in direct visual examination of skulls.

GEOGRAPHIC VARIATION: Quantitative analyses indicated notable geographic variation between samples of *Heteromys catopterius* from western vs. central portions of its range (appendix 3). Means for most variables were significantly different in univariate comparisons of specimens from Rancho Grande (locality 137) with those from Humboldt (locality 156). Externally, all variables but tail length ($P = 0.057$) were significant ($P <$

TABLE 3

**Results of Principal Components Analysis of Interspecific Variation Between *Heteromys anomalus* and *H. catopterius* Based on Specimens in All Age Classes from Los Canales de Naiguatá (see fig. 11)**

Elements of the unit eigenvector and loadings are presented for the first three principal components. Nine cranial measurements were transformed to their natural logarithms (ln) before computation of the covariance matrix and extraction of components. Eigenvalues (multiplied by 100) and the percentage of variation among specimens explained are given for each axis.

| | Unit eigenvector | | | Loadings | | |
|---|---|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC1 | PC2 | PC3 |
| ln-Occipitonasal length | −0.401 | 0.045 | −0.043 | −0.989 | 0.032 | −0.016 |
| ln-Zygomatic breadth | −0.287 | −0.219 | 0.133 | −0.933 | −0.205 | 0.066 |
| ln-Rostral length | −0.501 | 0.173 | −0.081 | −0.985 | 0.098 | −0.024 |
| ln-Nasal length | −0.529 | 0.531 | 0.000 | −0.955 | 0.275 | 0.000 |
| ln-Least interorbital constriction | −0.298 | −0.496 | 0.308 | −0.870 | −0.417 | 0.138 |
| ln-Squamosal breadth | −0.214 | −0.079 | 0.185 | −0.916 | −0.097 | 0.121 |
| ln-Maxillary toothrow length | −0.199 | −0.419 | −0.860 | −0.742 | −0.450 | −0.491 |
| ln-Parietal breadth | −0.101 | −0.433 | 0.291 | −0.546 | −0.672 | 0.240 |
| ln-Skull depth | −0.204 | −0.153 | 0.144 | −0.910 | −0.197 | 0.099 |
| Eigenvalue (× 100) | 4.704 | 0.389 | 0.110 | | | |
| % variation explained | 86.7 | 7.2 | 2.0 | | | |

0.003 for significant comparisons; test for mass not possible). The populations did not differ in median for the tail length/head-and-body length ratio ($P$ = 0.414). Comparisons of cranial measurements indicated that averages were significantly different for all measurements but rostral length and maxillary toothrow length ($P$ = 0.051 for MTR; $P$ = 0.025 for RL, not significant after correction for multiple comparisons; $P$ < 0.006 for

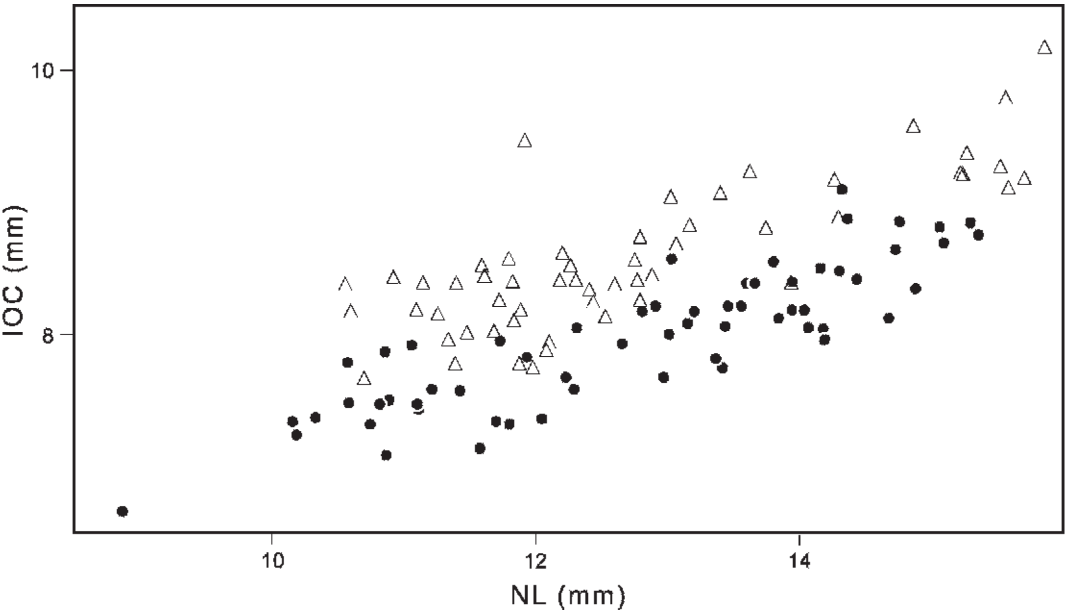

Fig. 12. Plot of least interorbital constriction vs. nasal length for specimens of *Heteromys* in all age classes from Los Canales de Naiguatá (localities 120 and 160). Circles represent individuals of *H. anomalus*, and triangles denote those of *H. catopterius*. Note that specimens of *H. catopterius* have a wider interorbital constriction than those of *H. anomalus*, relative to the length of their nasals.

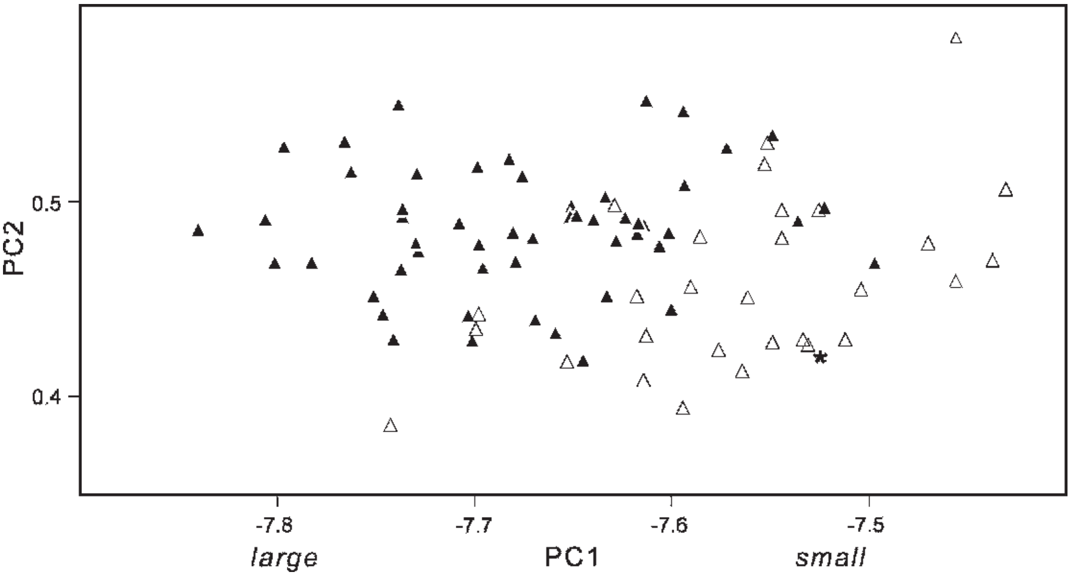

Fig. 13. Plot of specimen scores on the first two axes of a principal components analysis of nine cranial measurements of adult specimens of *H. catopterius* in age class 4 from throughout the range of the species. Solid triangles denote specimens from Estado Carabobo and western Estado Aragua; open triangles indicate specimens from eastern Estado Aragua as well as those from Estado Miranda, Estado Vargas, and Distrito Capital; and the asterisk represents the lone specimen from Estado Monagas. PC1 represents a size axis (with larger specimens appearing toward the left side of the plot), and PC2 constitutes a shape difference (see text and table 4).

significant comparisons). For all variables with a significant difference, the sample from Rancho Grande averaged larger than the one from Humboldt.

Multivariate morphometric analysis also showed substantial differences between westernmost populations vs. central and eastern ones. A plot of scores on the first two principal components of the PCA undertaken on all available specimens of *Heteromys catopterius* in age class 4 (using all cranial measurements but interparietal width and interparietal length) summarized morphometric variation within the new species (fig. 13). Only moderate overlap existed between specimens from westernmost populations (from Estado Carabobo and western portions of Estado Aragua, in the vicinity of Rancho Grande) vs. those from the El Ávila massif (the central portion of the species' distribution; figs. 1, 4). The lone available specimen from Estado Monagas in northeastern Venezuela (from the Macizo Oriental) lay within the cloud of specimens from El Ávila. Specimens from geographically intermediate populations in eastern Estado Aragua, western Estado Miranda, western Estado Vargas, and western Distrito Capital (e.g., Alto Ñeo León, Pico Codazzi, and El Laurel; appendix 1) tended to group with the central populations (from the El Ávila massif). These geographically intermediate populations lie to the west of the depression separating the El Ávila massif from the main Aragua-Carabobo chain of the Serranía del Litoral; this depression is marked by the courses of the Quebrada Tacagua and the Río Guaire. Individuals from the Serranía del Interior also fell with this group (Campamento Rafael Rangel; east-central Estado Aragua). The coefficients and loadings of PC1 all possessed the same sign, signifying that it represented a size axis (with larger specimens showing lower scores, because the signs of all the coefficients were negative; table 4). In contrast, PC2 constituted a shape axis (because some coefficients were positive and others negative; table 4). Here (as in the PCA for Los Canales de Naiguatá), PC2 represented a contrast between occipitonasal

TABLE 4

**Results of Principal Components Analysis of Geographic Variation in *Heteromys catopterius* Based on Adult Specimens in Age Class 4 from throughout the Range of the Species (see fig. 13)**

Elements of the unit eigenvector and loadings are presented for the first three principal components. Nine cranial measurements were transformed to their natural logarithms (ln) before computation of the covariance matrix and extraction of components. Eigenvalues (multiplied by 100) and the percentage of variation among specimens explained are given for each axis.

| | Unit eigenvector | | | Loadings | | |
|---|---|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC1 | PC2 | PC3 |
| ln-Occipitonasal length | −0.324 | −0.238 | −0.086 | −0.895 | −0.279 | −0.080 |
| ln-Zygomatic breadth | −0.375 | 0.194 | 0.020 | −0.903 | 0.197 | 0.016 |
| ln-Rostral length | −0.367 | −0.461 | −0.093 | −0.830 | −0.441 | −0.071 |
| ln-Nasal length | −0.427 | −0.468 | 0.065 | −0.851 | −0.394 | 0.044 |
| ln-Least interorbital constriction | −0.452 | 0.201 | 0.210 | −0.876 | 0.165 | 0.138 |
| ln-Squamosal breadth | −0.230 | 0.265 | 0.208 | −0.724 | 0.353 | 0.222 |
| ln-Maxillary toothrow length | −0.249 | 0.343 | −0.880 | −0.598 | 0.348 | −0.715 |
| ln-Parietal breadth | −0.202 | 0.475 | 0.310 | −0.593 | 0.590 | 0.308 |
| ln-Skull depth | −0.277 | 0.143 | 0.145 | −0.843 | 0.184 | 0.149 |
| Eigenvalue (× 100) | 0.847 | 0.152 | 0.097 | | | |
| % variation explained | 66.0 | 11.8 | 7.6 | | | |

length, rostral length, and nasal length vs. zygomatic breadth, least interorbital constriction, squamosal breadth, maxillary toothrow length, parietal breadth, and skull depth. Specimens with smaller values for the former three measurements relative to their values for the latter ones showed larger (more positive) scores on this axis.

Visual morphological observations indicate that subtle differences exist between the westernmost populations of *Heteromys catopterius* and the central and eastern populations of the species, but geographically intermediate localities appear to show transitional morphologies. Specimens from localities in Estado Carabobo and from the Rancho Grande region of Estado Aragua are generally larger and relatively wider than those from the El Ávila massif and from the Macizo Oriental, which are more elongated in shape (but not as much as *H. anomalus*). In addition, the rostrum is more developed and parallel sided (not anteriorly tapering) in western populations, in contrast to the somewhat less massive and slightly tapering rostrum typical of central and eastern populations. Two further differences distinguish the Rancho Grande population from that of Humboldt: (1) the molars appear larger and more robust in Rancho Grande than in Humboldt and (2) at Rancho Grande, the anterodorsal lobe of the periotic capsule of the mastoid is large, causing a distinct undulation in the posterior border of the squamosal, whereas this lobe is small at Humboldt, not causing a notable undulation in the posterior border of the squamosal. Despite these noteworthy differences between specimens from the two regions, individuals from sites geographically between Rancho Grande and Humboldt, in eastern Estado Aragua, western Estado Miranda, western Estado Vargas, and western Distrito Capital (e.g., Pico Codazzi, Alto Ñeo León; appendix 1), exhibit intermediate morphologies but generally match the central and eastern populations more closely than they do the more-western populations. Finally, one character distinguishes the populations in the Macizo Oriental from all others: individuals there possess very soft dorsal pelage, in contrast to the spiny pelage of western and central populations.

NATURAL HISTORY: Published studies and field notes provide rich and varied ecological information on *Heteromys catopterius*. Most of the available information corresponds to two sites where it has been collected in large numbers in the Serranía del Litoral (fig. 1): the vicinity of Rancho Grande in Estado

Fig. 14. Habitat of *Heteromys catopterius* at Rancho Grande (locality 137), Estado Aragua, Venezuela, taken just above the Estación Biológica. Photographed by Eliécer E. Gutiérrez in January 2008.

Aragua and the area surrounding Hotel Humboldt on the El Ávila massif along the border between Estado Miranda and Estado Vargas. Further information derives from sites in the Río Morón drainage on the northern slopes of the Cordillera de la Costa in Estado Carabobo (Bisbal-E., 1993). Unfortunately, the extensive morphological, reproductive, developmental, and behavioral information for *Heteromys* at Los Canales de Naiguatá in Estado Vargas in the Serranía del Litoral presented by Valdez et al. (1985) derives from a pooling of approximately equal numbers of *H. catopterius* and *H. anomalus* (appendix 1); future reanalysis of those data could provide fascinating insights into the ecology of the two species at this site of sympatry, but natural history information from that site is not included here.

At Rancho Grande near the crest of the main range of the Serranía del Litoral in Estado Aragua (fig. 14), field notes and specimen tags indicate that the species was captured commonly in various forested habitats but not in grassy and brushy areas. In the region surrounding the Estación Biológica de Rancho Grande (localities 131, 132, 136, and 137, Estado Aragua), Charles O. Handley, Jr. and Daniel I. Rhymer (assisted occasionally by John P. Rood) caught *H. catopterius* frequently in several habitats in March and April of 1960 (C.O. Handley, Jr. field notes, 1960; specimen tags). These habitats include: (1) an area of secondary vegetation below the Estación Biológica in an abandoned coffee and banana farm (although traps were placed there in areas grown up with weeds, grass, and brush, as well as in ‘‘dry’’ forest, evidently *Heteromys* were captured only in the forested areas, termed ‘‘deciduous forest’’ on specimen tags); (2) a forested (presumably evergreen) area on the slope behind the Estación Biológica along the ‘‘water trail’’ (see map in Beebe and Crane, 1947: 48; (3) forested areas (including cloud forest) at El Portachuelo, slightly below and west of the Estación Biológica; and (4) cloud forest on Pico Limón. Although traps were placed in grassy areas near the Estación Biológica, *Heteromys* was not captured there.

The month following completion of work at Rancho Grande by Handley and Rhymer, John P. Rood conducted capture-recapture sampling and laboratory experiments at Rancho Grande that provide extensive information regarding the ecology, behavior, and development of *Heteromys catopterius* (Rood, 1963; Rood and Test, 1968). Rood collected a few voucher specimens from these trapping grids and adjacent areas (see Rood and Test, 1968); all that we have examined represent *H. catopterius* (appendix 1). Approximately half derive from cloud forest, but others were captured in a forest near a small stream, a second-growth forest, second growth at the edge of tall grass, and a clump of tall grass near second-growth forest (J.P. Rood field notes, 1960). Although some of the individuals in Rood's studies may have been *H. anomalus* (which has been captured occasionally at Rancho Grande; see Sympatry and Zones of Contact with *Heteromys anomalus*), at least the vast majority probably were the species now known as *H. catopterius*.

Rood sampled two areas using traps arranged in grids (Rood and Test, 1968: 90–92). Area 1 comprised a mosaic of secondary habitats in a former coffee plantation, including grass, *Heliconia*, bamboo, short trees, and *Cecropia*, as well as primary cloud forest. In contrast, area 2 was mature cloud forest. There,

> the tree canopy was composed of two layers, the upper of *Gyranthera* [a tall buttressed tree in the family Malvaceae], the stilt palm *Iriartea*, and other large trees about 50 m tall and averaging some 8 m apart, while the lower included tree ferns, other palms, and small trees about 7 m high and averaging perhaps 2 m apart . . . the green ground cover of dwarf palms (*Geonoma*), ferns, small bushes and herbaceous plants was sparse, and the forest floor relatively open. Leaf litter was patchy . . . however, there were many shelters for small mammals in the form of fallen small trees and large branches, tangles of fallen small branches, large frond-like dead leaves of *Iriartea*, the bases of stilt palms, and the closely clustered aerial roots of another palm. (Rood and Test, 1968: 91–92)

The two areas showed differing patterns of capture of *Heteromys*. In area 1, trap success was highest in cloud forest and *Heliconia*, although moderate numbers of captures were also recorded in *Cecropia* and grass and a few in bamboo and secondary forest. In area 2, captures were more evenly distributed across the grid (which was entirely within cloud forest), and the trapping there yielded a higher number of unique individuals (Rood and Test 1968: 93–94).

Rood's fieldwork and observation of individuals in captivity provide some information regarding reproduction and development of *Heteromys catopterius*. Although trapping occurred only over a few weeks, the observed patterns indicated a possible peak of reproductive activity in April and May (corresponding to the onset of the rainy season; Rood, 1963: 189; see also Rood and Test, 1968: 94–96). Copulation was observed once in captivity (Rood, 1963: 189). Based on a small sample size, litter size varied from 1 to 3, and mass at birth averaged 3.3 g. Major events in the development of *H. catopterius* (measured in captivity) include: ears opened on day 5, biting (when handled) commenced on day 10, dorsal hair became apparent on day 11 (when the individuals weighed 13.7 g), walking and eating solid food began at 20 days (when individuals had full juvenal pelage, but their eyes were still closed; average weight at the time was 21.4 g), but nursing continued to day 48 (when observation ceased; Rood, 1963: 190).

*Heteromys catopterius* consumed a wide variety of native and exotic foods. In captivity, it ate corn especially readily but also consumed avocados, tomatoes, bread, dried cereals, rolled oats, cabbage, and cheese. The nut of the stilt palm (*Iriartea*) was found in live-traps along with *Heteromys*, presumably brought there in the animal's cheek pouches. This nut was eaten readily by captive animals, as well as several other foods found naturally in the surrounding environment: "spiny palm roots (*Bactris*), seeds and blades of an unidentified sedge, roots and blades of grasses, and fruits of *Passiflora*, the candela tree (*Gyranthera caribensis* Pittier), and several others which could not be identified" (Rood, 1963: 188). In captivity, the mice used their cheek pouches to bring corn to nest (Rood, 1963: 188–189), and while eating, "the rats did not hold the food in their front paws, as do many other rodents, but rested it on the ground supported by the forepaws" (Rood, 1963: 189).

A few individuals were brought into captivity in the Estación Biológica and housed in elaborate experimental conditions, where nesting and digging comprised noteworthy activities. After housing individuals in cages, Rood moved some to a study room measuring 17 × 18 feet,

> prepared for the *Heteromys* in an attempt to provide conditions as similar as possible to those under which the animals lived in the wild. The floor was covered with soil to a depth of 1/2 inch. Mounds two feet deep were placed in the corners to give the animals opportunity for digging and the whole floor covered with a layer of leaf litter. One of the corners was planted with grass four feet high and another with ferns and small herbs. Palm branches were piled in the center of the room forming a brushpile. (Rood, 1963: 187)

In that environment, *Heteromys catopterius* was observed making nests and digging. Individuals

> made globular nests approximately six inches in outside diameter. In the study room where fresh and dead leaves, grass, and ferns were provided, the dead leaves were selected as nesting material and chewed into pieces four inches by two inches or smaller, which were transported in the cheek pouches. These nests were placed in the corners of the room or under the brushpile. The mice occasionally dug short tunnels in the soil banked in the room corners. Digging was done entirely with the front feet and these were used to push the loosened dirt to the surface with the palm directed outwards. (Rood, 1963: 188)

Observations by Rood also offer information regarding behavior and locomotion of the species. Adult males showed aggression toward humans, but neither adult females nor juveniles of either sex did. Adult males exhibited aggression toward females unless the latter were in estrus (Rood, 1963: 187, 191). A clear dominance structure existed, especially in the context of intraspecific competition for nests in captivity: adult males were dominant over adult females and juvenal males; and adult females over juvenal males. Dominance among adult males was determined via brief fights (Rood, 1963: 191). The mice were typically nocturnal (Rood, 1963: 188; Rood and Test, 1968: 96). Information regarding locomotion is contradictory, including the observation that individuals "run with rapid bounds and the tail does not drag" (Rood, 1963: 188) but that locomotion was "remarkably inept or phlegmatic. Their movements, mostly hops, were usually slow." (Rood and Test, 1968: 98).

For areas near Hotel Humboldt in Estado Miranda and Estado Vargas (locality 156) near the crest of the El Ávila massif of the Serranía del Litoral, field notes provide detailed ecological information for *Heteromys catopterius*. There, the species inhabits primary cloud forests, especially in association with palms. Merlin D. Tuttle and several other workers sampled this region in August and September of 1965 (see also Handley, 1976). The macrohabitat of the species at that site can be characterized as follows (M.D. Tuttle field notes, 1965):

> Primary forest . . . 35–65 ft [11–20 m] tall (tallest trees in stream valley), very damp with a very lush growth of moss on all the trees and vines. Many of the trees are palms 25–35 ft [8–11 m] tall which have profuse root systems about 2–3 ft [0.6–0.9 m] in diameter and 2–3 ft [0.6–0.9 m] above the ground, providing good cover. Otherwise, much of the area has fairly sparse ground cover. Bamboo is sparse to dense over the area. Along the stream, there are many mossy rocks. Ferns, moss and vines are common to the area. There are some tree ferns and many epiphytic plants. The forest is generally quite dense . . . dripping with moisture condensed from frequent low clouds . . . . The entire area is fairly dense, and there are dense-to-sparsely scattered palms over the entire area. The whole area is very wet and has usually been engulfed in dense clouds.

Furthermore, Tuttle noted that: "*Heteromys* [were] especially associated with areas of palms . . . some were in rock cover, and about the same number were in bamboo cover below the palm trees . . . [many were found] in the forest where palms were dense to at least scattered . . . (in contrast to *O. albigularis* [= *Nephelomys caracolus*], which seem to occur wherever there is forest)." Indeed, several species of small nonvolant mammals (but no *Heteromys*) were captured in trap lines at similar elevations in (1) forest with bamboo understory (but few or no palms); (2) forest with disturbed understory (ferns, grass, moss, etc., but few or no palms); and (3) grassy areas.

Detailed microhabitat information for *Heteromys catopterius* at Hotel Humboldt is available as well (M.D. Tuttle field notes, 1965). The species was most commonly captured in association with palms, especially at the bases of palm trees with stiltlike root clumps: in a dense growth of palms (2 individuals); in a dense palm forest 15 ft [5 m] tall; on the ground around the palms (in a palm forest about 30 ft [9 m] tall, where there were also other species of trees that reached at least 60 ft [18 m]; (3 individuals); at the base of a palm tree (2 individuals); at the bases of palm trees in the forest; at the base of a palm tree in forest 30 ft [9 m] tall; at the base of a palm where there was a dense growth of young palms and saplings 15 ft [9 m] tall; at the bases of palm trees in the forest (there are large root masses above the ground at the bases of each palm providing good cover; 3 individuals); in the root clump of a palm tree; in the roots of a palm in dense palm forest; at the root clump base of a palm tree in the forest; at the root clump bases of palms (2 individuals); in the root clumps of palms in the forest (2 individuals).

The species was also trapped in areas with bamboo, and these areas often also contained palms (M.D. Tuttle field notes, 1965): in dense bamboo; in dense bamboo in forest; in dead leaves in bamboo about 3 ft [0.9 m] tall in forest; under rocks in grass and bamboo in forest; in a dense mixture of bamboo, vines, and ferns; in a dense mixture of bamboo, vines, and ferns in the forest; in dense bamboo beneath palms; in dead leaves and low bamboo in scattered palms; in a root clump of a palm in a dense mixture of grass and bamboo; in a dense mixture of bamboo, vines, ferns, and other plants about 4 ft [1.2 m] tall; in a dense mixture of bamboo, vines, ferns, etc., about 5 ft [1.5 m] tall in the forest; in a mixture of bamboo, vines, ferns, and young palms in the dense forest; in mixture of bamboo, vines, ferns, and young palms about 6 ft [1.8 m] tall in forest of scattered palms mixed with other trees.

The species was occasionally found associated with rocks or logs, but only rarely in grass or other microhabitats (M.D. Tuttle field notes, 1965): in rocks; in rocks in the forest; under a rock in dense forest; on mossy rocks in the forest (3 individuals); under large mossy rocks in the forest near the stream; under fallen trees (2 individuals); in a hollow tree in dense forest; on the trunk of a leaning tree in dense forest 45 ft [14 m] tall; on a dead log 8 ft [2.4 m] above the stream and spanning a distance of 25 ft [8 m] from one side to the other, on one side there was dense bamboo, and on the other a mixture of dense ferns and young bamboo (the forest above was up to 60 ft [18 m] tall); in dense grass a short distance from the palm forest; in dense grass about 1.5 ft (0.5 m) tall near the stream in a slightly open part of the forest; in dense vines 6 ft (1.8 m) from the stream; at the entrance to a hole under a root ledge.

At Hotel Humboldt, the species only occasionally was recorded to have held items in its cheek pouches (M.D. Tuttle field notes, 1965). Two individuals were taken carrying palm nuts 26 × 22 mm in their pouches. Each had one nut, and one of them also had half a millipede in its pouch with the nut. A third individual had a palm nut 27 × 20 mm in its pouch.

Further information regarding the natural history of *Heteromys catopterius* derives from the results of surveys conducted in the Río Morón drainage on the northern slopes of the Cordillera de la Costa in Estado Carabobo. Francisco J. Bisbal-E. and colleagues (Sergio Bermúdez, José Daniel P. Bora, Arnaldo Ferrer, Alfredo Lander, Alejo Ospino, and Ramón Rivero) undertook a general inventory of vertebrates in the Río Morón drainage in 1990–1991, including trapping for small nonvolant mammals (Bisbal-E., 1993). Much of the region had been cultivated for many years, but in 1971 an effort began to return the area to a more natural state for the purpose of restoring water supply to small towns and a large industrial complex on the coast. Although not all captured individuals were collected, all the voucher specimens of *Heteromys* that we have examined from this work represent *H. catopterius* (from La Justa and Palmichal; appendix 1). *Heteromys catopterius* was one of the most commonly captured species in both cloud forest and semideciduous forest in this area, and it inhabited some secondary areas in addition to primary forest (Bisbal-E., 1993).

At La Justa (300–400 m; locality 141), *Heteromys catopterius* and *Proechimys guairae* were the most commonly captured small, nonvolant mammals. The macrohabitat at La Justa was recovering semideciduous forest. The area had been cultivated for coffee, cocoa, and other crops for many years, but the croplands had been abandoned, leading to the formation of secondary forest before the inventory work commenced. The forest had a ''fairly dense but irregularly distributed shrub layer, due to differing light conditions within the forest, and [overall, the forest had] two or three dense strata with an average height of 15–20 m'' (Bisbal-E., 1993: 366; translation ours).

At Palmichal (700–1000 m; localities 143 and 144), *Heteromys catopterius* and *Oryzomys albigularis* (= *Nephelomys caracolus*) constituted the most commonly captured small, nonvolant mammals. The macrohabitats at Palmichal included both primary and secondary cloud forests. The latter were abandoned coffee plantations and small plots of subsistence agriculture that had regrown by the time of the inventories. The cloud forest ''has an average height of 20–25 m with emergent trees reaching 30–40 m; it has 2–3 strata and a well-developed understory. Epiphytes are abundant on higher branches and treetops, whereas lianas are rare'' (Bisbal-E., 1993: 366; translation ours). At both La Justa and Palmichal, *H. catopterius* was captured only on the ground, despite the placement of traps on tree branches as well.

SYMPATRY AND ZONES OF CONTACT WITH *HETEROMYS ANOMALUS*: Presently available specimens indicate that *Heteromys catopterius* and *H. anomalus* show largely complementary distributions in north-central and northeastern Venezuela. Apparently, the distributions of the two species are generally parapatric, with only very narrow zones of sympatry. In general, *H. catopterius* inhabits higher, wetter areas than *H. anomalus*. Known sites of contact between the species occur in the Rancho Grande region in the western portion of the Serranía del Litoral, the El Ávila massif of the Serranía del Litoral, the Tiara region of the Serranía del Interior, and the Caripe region of the Macizo Oriental (figs. 1, 4). Similar parapatric distributions have been observed for several other pairs of species in the subfamily (Genoways, 1973; Rogers and Engstrom, 1992; Anderson, 1999; Anderson and Jarrín-V., 2002; Anderson and Timm, 2006).

The most detailed distributional information for an area of geographic contact between *Heteromys catopterius* and *H. anomalus* derives from the Rancho Grande region (in the western portion of the Serranía del Litoral). There, the distributions of the two species meet on both the southern and northern slopes. On the southern slope, the species' distributions come into contact at ca. 1050 m. Many specimens of *H. catopterius* from the Rancho Grande region correspond to areas near the Estación Biológica de Rancho Grande and El Portachuelo. El Portachuelo (locality 136) lies at the crest of the range and represents a pass between Pico Periquito and Pico Guacamaya. The Estación Biológica (localities 47 and 137) lies on the southern slope, slightly higher than and just to the east of El Portachuelo. Near the Estación Biológica and El Portachelo, *H. catopterius* was captured in large numbers in cloud forests and secondary forests (see Natural History; C.O. Handley, Jr. field notes, 1960). In contrast, only a few specimens of *H. anomalus* exist from areas near the Estación Biológica. One was collected by William Beebe; it was taken in an unspecified habitat within 1 km of the Estación Biológica (Tate, 1947). The Smithsonian Venezuelan Project collected three *H. anomalus* from areas slightly below the Estación Biológica on the southern slope; most of the sampling was in secondary habitats, especially in and near a ''banana grove with thick underbrush and tall tress'' (N.E. Peterson field notes, 1965). The tags for those specimens indicate that one was captured ''in dense herbs—coffee and banana growth'' and the other two in ''dense herbs and banana plants.'' In addition, the Smithsonian Venezuelan Project also collected an individual (USNM 371016) that shows a mixture of morphological characters of the two species and may represent a hybrid between them. We provisionally identify it as *H. catopterius*, but genetic studies are necessary to examine the possibility of limited hybridization between the two species in this region intimated by the morphological data. This specimen derives from the same macrohabitat as the three individuals of *H. anomalus*, and the tag indicates the microhabitat as at the "base of sapling, low herbs." Interestingly, *H. catopterius* was captured in an area *below* the Estación Biológica on the southern slope along a stream in rainforest habitat (habitat described and pictured in Voss, 1988: 417–420; R.S. Voss field notes, 1979). Taken together, the available natural history information suggests that the two species likely segregate by habitat type (*H. catopterius* in wetter and/or more mature habitats and *H. anomalus* in drier and/or more disturbed areas) at a local scale in this area.

Records also document the presence of both species from the northern slope of the Serranía del Litoral just north of El Portachuelo and Rancho Grande. Researchers from the Museo del Instituto de Zoología Agrícola (Universidad Central de Venezuela) in Maracay surveyed small mammals at many elevations along the highway that passes by Rancho Grande and leads to Ocumare de la Costa. Both *Heteromys catopterius* and *H. anomalus* have been documented from 900–920 m on the northern slope (localities 45 and 130); in addition, *H. anomalus* is known from 630 m (locality 44), and *H. catopterius* from 680 m (locality 129). No habitat information accompanies these records.

Additionally, two sites of sympatry and one site of near parapatry exist in the central portion of the range of *Heteromys catopterius*. The two species come into geographic contact on the northern slopes of the El Ávila massif (in the central portion of the Serranía del Litoral). There, both species have been collected in very large numbers at Los Canales de Naiguatá, at 720–800 m (localities 120 and 160; see Valdez et al., 1985). Because these water-gathering canals span several kilometers, it is not clear whether or not the species coexist in the same macrohabitat or, alternatively, are separated by habitat and/or elevation. Specimens also document an area of geographic contact between the two species in the Tiara region of the Serranía del Interior. The species are sympatric at Campamento Rafael Rangel (= Loma de Hierro/Minas de Niquel; localities 53 and 138) at 1260 m, but no habitat information exists for any of the specimens. *Heteromys catopterius* exists from 1200 m at the same site, and *H. anomalus* occurs at nearby localities of La Horqueta (locality 51) and Agua Amarilla (locality 52), at slightly lower elevations (ca. 1080–1100 m). At the eastern end of the main Aragua-Carabobo chain of the Serranía del Litoral, the two species come into close geographic contact, although no known site of sympatry exists. Here, *H. catopterius* inhabits El Laurel (locality 155) at 1355 m, and *H. anomalus* occurs at the nearby sites Turgua (1144 m; locality 76) and Bosquecillo, on the campus of the Universidad Simón Bolívar (ca. 1100 m; locality 75).

Finally, the two species come into geographic contact in the Caripe region of the Macizo Oriental. There, two very nearby sites of sympatry exist: La Laguna (1330 m for *Heteromys anomalus* and 1170–1335 m for *H. catopterius*; localities 84 and 159 for *H. catopterius*) and an area sampled near San Agustín (1180–1260 m for *H. anomalus* and 1170–1180 m for *H. catopterius*; localities 84 and 159). In addition, *H. catopterius* occurs at two nearby sites (San Agustín, 1270 m and Hacienda San Fernando, 1320 m; localities 157 and 158), and closeby, *H. anomalus* is known from the Cueva del Guácharo (1060–1065 m; locality 86). Finally, two specimens (USNM 409820 and 409821) from Cueva del Guácharo (1010 m) display a mixture of characters of the two species; although provisionally we ascribe them to *H. anomalus*, they may constitute rare hybrids between the two species. Future genetic studies in the region are necessary to address this possibility. In contrast to the well-documented area of contact between the two species in the region of Rancho Grande (see above), the few available records from near Caripe do not allow for any clear characterization of habitat-related, successional, and/or elevational separation between the two species.

CONSERVATION STATUS: *Heteromys catopterius* probably faces minimal risk of extinction or even population-level decline in most of its range. Like most species of the genus, data available from field collectors indicate that the species inhabits only closed-canopy evergreen forests (i.e., not deciduous forests, xerophytic vegetation, natural grasslands, or open agricultural areas). Among the evergreen montane forests it inhabits, the species appears especially associated with cloud forests and with areas holding an abundance of palms. Fortunately, it shows substantial tolerance for disturbance within forested ecosystems. In addition to particularly frequent collection in mature cloud forests, the species also has been trapped in large numbers in secondary forests (e.g., at Rancho Grande; see Natural History). In addition, *H. catopterius* exhibits a moderately widespread distribution (throughout most of the Cordillera de la Costa). Finally, many national parks and other governmentally protected reserves harbor known localities of the species: Parques Nacionales El Ávila, El Guácharo, Henri Pittier, Macarao, Miguel José en Sanz San Esteban; and Monumentos Naturales Cueva del Guácharo and Pico Codazzi). *Heteromys catopterius* also has been documented from private lands conserved as a natural watershed in the Río Morón drainage (Bisbal-E., 1993). The protection afforded these reserves varies greatly, but large areas of intact forest remain in several of them (perhaps most notably the Parque Nacional Henri Pittier and Parque Nacional El Ávila).

### *Heteromys anomalus* (Thompson, 1815)
### Caribbean Spiny Pocket Mouse

DISTRIBUTION: Distributed across much of northern Colombia and Venezuela and in the upper Río Magdalena Valley of central Colombia, from near sea level to middle elevations; also inhabits the nearby Caribbean islands of Margarita, Trinidad, and Tobago (figs. 1, 4; Anderson, 2003b; appendices 1 and 2). In addition to regions dominated by forest, *H. anomalus* also inhabits restricted forested areas (riparian gallery forests) in the *llanos* (savanna) of Venezuela (August, 1984; Soriano and Clulow, 1988). The species typically ranges from sea level to ca. 1600 m in elevation, although its upper distributional limit is lower in some mountain ranges (e.g., the Cordillera de la Costa in Venezuela; see Biogeography of *Heteromys catopterius* and *H. anomalus*); a population in the semi-isolated Macizo de Guaramacal in western Venezuela inhabits an anomalously high elevation (2430 m; Anderson, 2003b). Note also seven localities of *H. anomalus* in the central and western *llanos* of Venezuela reported by Utrera et al. (2000); we have examined vouchers only from one of those sites (Caño Hondo, locality 66, appendix 1); the remainder probably represent new records of *H. anomalus*.

DIAGNOSIS: A species of spiny pocket mouse with adults showing the following combination of characters (figs. 6, 7, 9): p4 (lower permanent premolar) with three lophids; P4 (permanent upper premolar) with straight, moderately long fold in anterior margin of posterior loph; tubercle or swelling at posteroventral border of infraorbital foramen absent; mesopterygoid fossa formed by long, thin hamular processes of pterygoids; optic foramen especially small, with posterior margin formed by strong bar of bone; parietomastoid suture dipping well ventral to parietal crest posterior to its widest point, then ascending dorsally to rejoin crest near its posterior termination; rostrum moderately long and generally moderately tapered anteriorly, without anterodorsal flare; anterior portion of premaxillary convex (inflated), forming a smooth (not stepped) lateral border of rostrum; interorbital constriction narrow; braincase narrow and not inflated; interparietal variable in size and shape; skull average for genus (ONL 31.06–39.02 mm in adult specimens of age class 4; table 1, appendix 3); dorsal pelage typically pale brown strongly grizzled with thin ochraceous hairs intermixed among spines, but occasionally almost uniformly dark drab gray (in wet lowlands of Estado Zulia, in some parts of the Cordillera de Mérida, in mesic areas of Estado Monagas and Estado Sucre, and on the island of Tobago), usually harsh and spiny, but often softer in montane regions; weak patch of dark coloration present on dorsal and external surfaces of forearms, continuous with dark coloration of flanks; ears distinctively rounded, brown to gray and large relative to body size; orange band on flanks absent; tail typically strongly bicolored and slightly to moderately longer than head-and-body length; plantar surface of hind feet naked.

KARYOLOGY: Engstrom et al. (1987) reported the standard karyotype of 2n = 60, FN = 68 for 20 individuals of *H. anomalus* from Estado Miranda (24 km N Altagracia de Orituco and 25 km N Altagracia de Orituco, localities 79 and 80), Estado Monagas (Caripito, locality 88) and Estado Sucre (40 km SW Caripito, locality 104), with voucher specimens deposited at the TCWC and CM. Although those authors did not provide museum catalog numbers for the specimens that were karyotyped, we have examined specimens from three of these localities in those museum collections (appendix 1); all represent *H. anomalus*.

COMPARISONS: See above for comparisons with *Heteromys catopterius*, and Anderson (2003b) and Anderson and Timm (2006) for comparisons with other species of the genus.

GEOGRAPHIC VARIATION: Although a comprehensive review of geographic variation in the widespread *Heteromys anomalus* lies beyond the scope of the current work, some noteworthy patterns exist. Externally, a few populations in mesic areas (e.g., wet regions of Estados Lara, Monagas, Sucre, and Zulia in Venezuela, and on the island of Tobago) show darker, less grizzled dorsal pelage than populations in most parts of the species' range (see also Anderson, 2003b). One doubly insular population (Bush Bush Forest; locality 22) exhibits markedly smaller size than other examined populations (Anderson, 2003b). It corresponds to the tiny island of the same name, which lies within the Nariva Swamp in central-eastern Trinidad (Downs et al., 1968).

NATURAL HISTORY: Field notes and published studies provide substantial ecological information on *Heteromys anomalus* from a few sites where it was collected in large numbers in eastern Venezuela and Trinidad and Tobago. However, as mentioned above (see account of *H. catopterius*), the extensive information provided by Valdez et al. (1985) for the genus at Los Canales de Naiguatá in Estado Vargas in the Serranía del Litoral corresponds to pooled data for *H. anomalus* and *H. catopterius* (localities 120 and 160; appendix 1); we do not include natural history information from that site here. See Anderson (2003b) for summaries of natural history information for sites in Colombia and western Venezuela.

On the slopes of the Macizo Oriental (fig. 1) in Estado Monagas and Estado Sucre, field notes indicate that *Heteromys anomalus* was captured commonly in intact tropical rainforest adjacent to cropland but only occasionally in drier areas more dominated by agriculture. G.H.H. Tate and H.J. Clement sampled several sites in this region in March–May 1925 (see also Tate, 1931). The area at Neverí (locality 111) where *H. anomalus* was common, was:

> entirely covered with splendid forest, and although dry at present, I judge that it has a very severe rainy season from the luxuriance of its clothing of vegetation. It is only within the last few years indeed that a road has been made into the headwaters of the Neverí, and as yet clearings are not plentiful.... [Along the river] runways are plentiful, and the river-banks have a moderate slope, and are studded with large boulders, over-topped by giant forest and buried in a rich growth of *platanillos*. Toward the upper part of the line the banks become rather steeper, slatey outcroppings protruding their faces into the water-way...in steaming, rotting jungle.... [A] very abundant plant in the forest is a slender-stemmed moderately tall palm, which has its trunk quite clothed with long stiff, needle-pointed spines....'Elephant-ears' and great arboreal aroids are plentiful. (G.H.H. Tate field notes, 1925)

Latal (locality 113), another site where *H. anomalus* was common, "is surrounded by high hills all partly cleared in their lower slopes and planted to coffee. However there is much fine forest." (G.H.H. Tate field notes, 1925).

In contrast, *Heteromys anomalus* was captured only occasionally by Tate and Clement at San Antonio de Maturín (locality 89), a drier region with denser human settlement. The region as a whole holds "xerophytic vegetation, but far up the valley on either hand one can descry good looking forest." (G.H.H. Tate field notes, 1925). The valley floor was densely populated, and many pastures were present. The valley was drained by "a stony, broad, shallow stream meandering between alternate small bluffs and *playas*. Along this stream are also large stands of *caña lata*, the tall reed-like cane often used for walling in native houses where no strength is needed" (G.H.H. Tate field notes, 1925).

At Finca Vuelta Larga (locality 101) in the lowlands of Estado Sucre, field notes indicate that *Heteromys anomalus* was captured in areas of secondary evergreen forest as well as adjacent small agricultural plots, but not in inundated savannas of grasses and sparse shrubs. Robert S. Voss, Hernán C. Castellanos, and Carlos Gauveca-C. sampled these managed and seminatural habitats in August 1987 (R.S. Voss and H.C. Castellanos field notes, 1987; see also Voss, 1991). The area comprised a mosaic of inundated savannas (*estero*) and secondary forests (*mato*) at slightly higher elevations. Similar numbers of traps were set in inundated savanna and in forest, as well as a lesser number in small recently established agricultural plots (*conuco*). The savanna was flooded by use of a series of dikes and fenced for heavy grazing; shrubs and tall herbs grew along the fences, where most of the savanna traps were set. The forest was secondary growth, cleared ca. 14 years prior for small agricultural plots and allowed to regrow (abandoned *conuco*). The vegetation there was "a dense tangle of second-growth trees (mostly unbuttressed) and shrubs with many viny tangles" (R.S. Voss field notes, 1987). This secondary forest was evergreen and dominated by palms, with a variable and discontinuous canopy ca. 30 m high (H.C. Castellanos field notes, 1987). *Heteromys anomalus* was captured in secondary forest and recently established agricultural plots (*conuco*) but not in traps set in the wet, marshy savanna margins under fences, tall grass, and occasional shrubs.

Some information regarding the microhabitats of *Heteromys anomalus* at Finca Vuelta Larga is also available (R.S. Voss, H.C. Castellanos, and C. Gauveca-C. field notes, 1987; translations ours, where relevant): on the ground in leaf litter under dense undergrowth in forest; on bare ground under tangled lianas with leaf litter on top, and under stilt roots of a *Cecropia*; on ground in wet leaf litter under tall grass in old [abandoned] *conuco* (grass, bushes, plantains, and small trees); on ground in leaf litter and below a group of lianas that surround a palm (*Corozo*) 665 mm in dbh; on ground in tall grasses and shrubs (2 individuals).

The species may be an agricultural pest in at least some regions. In the original description, Thompson (1815) noted that "The habits of this tribe of rats are singular and curious: where numerous, they do incalculable mischief in barns and granaries; for, not satisfied with what they can eat on the spot, they stow away and carry off in their cheek pouches no inconsiderable quantity [of grain], to be deposited in their retreats for times when food is not to be procured from without" (Thompson, 1815: 162). We know of no studies quantifying the extraction of agricultural grain by *Heteromys anomalus*. Whereas the species does not inhabit large fields of mechanized agriculture (see Utrera et al., 2000; Anderson, 2003b), it does exist in many areas containing smaller fields in subsistence agriculture settings (see above), where it may be a pest to humans.

Substantial natural history information exists for *Heteromys anomalus* at a site in Trinidad where large numbers of the species were captured during surveys that spanned several years. Teams from the Trinidad Regional Virus Laboratory surveyed Bush Bush Forest (locality 22) for small, nonvolant mammals from 1960–1963 (Worth et al., 1968; see also Aitken et al., 1968). Downs et al. (1968) provide detailed information on the region, which we summarize here. Bush Bush Forest is the name given to the areas sampled on Bush Bush Island, a low, forested island present in the Nariva Swamp of central-eastern Trinidad. The island has sandy, well-drained soils and is approximately 0.25 mi (0.40 km) wide and 2–3 mi (3–5 km) long. Although most of the island itself is never flooded, it merges into areas that are seasonally inundated that support swamp forest comprised of palms and a few hardwoods. Most of the surrounding open swamp, however, is almost continuously inundated, covered by grass, cane, or aeroids. Before 1960, the island received only periodic visits by humans for fishing during the dry season, as well as sporadic visitation associated with hunting or selective extraction of timber. Both removal trapping and mark-recapture studies were undertaken; all voucher specimens that we examined from this work represent *H. anomalus* (appendix 1).

*Heteromys anomalus* was consistently one of the most commonly collected small, nonvolant mammals in nonflooded forested areas on Bush Bush Forest, and a variety of information regarding its natural history is available (Worth et al., 1968, from which the following information derives). Removal trapping spread over several parts of the island over four years yielded a total of 423 individuals of *H. anomalus*, with an overall trap success that varied from 0.3 % to 2.5 % in individual years. A general decline in numbers was observed during the study. Minimal trapping in swampy habitats failed to capture any *Heteromys*. Mark–recapture studies in the Restan area of Bush Bush Island captured 183 individuals (including recaptures) over three years, with much higher trap success (8.2%). The species showed a small home range, "rarely entering traps in more than two adjacent stations" that were set an average of ca. 100 ft (30 m) apart (Worth et al., 1968: 271). No individual of the species was found to have moved even 300 ft (91 m). Immature individuals were present in every month of the year but January, but were most frequent from May through October (the wet season). Some individuals were followed for more than six months. The species "tended to begin foraging earlier in the evening than other species" (of rodents and marsupials; Worth et al., 1968: 271).

Some behavioral information in captivity is available for individuals of *Heteromys anomalus* from the island of Trinidad. John F. Eisenberg conducted a landmark comparative study of behavior across the family Heteromyidae (Eisenberg, 1963). Most of his investigation of the genus *Heteromys* focused on *H. lepturus* (from Finca La Selva, Veracruz, Mexico; = *H. desmarestianus*; see Anderson et al., 2006, for geographic variation within the *H. desmarestianus* complex). In addition, however, four individuals of *H. anomalus* were surveyed for individual behavior and some aspects of intraspecific social behavior. These individuals were provided by the Trinidad Regional Virus Laboratories from an unspecified location, presumably in Trinidad. Individuals were held in terraria at high humidity with soil covering the floor. Observations were performed at night using a red light for illumination. In male-female encounters, *H. anomalus* was less aggressive than species of other heteromyine genera, with "chasing" constituting the primary aggressive behavior of *H. anomalus* (Eisenberg, 1963: 50, see also 68, 94). Both naso-nasal and naso-anal behaviors were observed between individuals of the opposite sex (Eisenberg, 1963: 51–52). Subsequently, preliminary sexual behaviors were observed, but copulation was not: "Driving [chasing and attempting to mount the female], perineal investigation, grooming, patting, and mounting [gripping of flanks of female with forelimbs, pressing ventrum against back of female and attempting intromission] were displayed by the males. A typical lordosis [freezing movement, allowing the male to mount as the female raises her hindquarters] was shown by the females.... The male *Heteromys* [*anomalus*] uses a neck grip [grasping with incisors the fur over the dorsal gland of the female during a mount]" (Eisenberg, 1963: 51, see also 47, 58).

On the island of Tobago, field notes document the capture of *Heteromys anomalus* near Charlottesville on the slopes of Pigeon Peak in several forested habitats (especially montane forest) but not in areas under active cultivation (locality 1; R.S. Voss and M.E. Holden field notes, 1989). Robert S. Voss and Mary Ellen Holden sampled a variety of habitats in this region in January 1989 (see also habitat descriptions and photographs in Voss, 1991: 73–76). *Heteromys anomalus* was the most commonly captured small nonvolant mammal in montane forests, whereas *Zygodontomys brevicauda* was the most common in most other sampled habitats. *Heteromys anomalus* was also captured occasionally in lowland primary rainforest (Voss, 1991) and abandoned cocoa plantations with an intact original canopy. The species was not caught in agricultural clearings (cocoa, plantains, pigeon peas, papaya, and cassava [manioc]) or in active cocoa plantations (R.S. Voss field notes, 1989). The montane forest where *H. anomalus* was especially common can be characterized as follows:

> This mature...forest is developed along the main ridge above about 1500 ft [457 m] elevations.... This part of the ridge is probably cloud-covered at least briefly on most days and so the vegetation is very wet and has a montane aspect despite the insignificant altitude. Physi-

> ognomically, this ridge-top forest at only 1600 ft [487 m] elevation has the appearance of Andean forests found at much higher elevations . . . . The forest along the ridge-top . . . is not very tall, the canopy only about 25–30 m or so, or even less in areas more exposed to the wind. The trees that form the canopy are also of much lesser girth than in lowland forests and are seldom buttressed . . . . Small, graceful *Euterpe* palms are much more abundant in these forests than below and often emerge into the canopy. The undergrowth is denser here than in lowland forests and includes seedling trees and woody shrubs as below, but large ferns and Cyclanthaceae are commonest. Gingers and *Heliconia* are present too. Small tree-ferns are common in a few situations. Many of the tree trunks support dense growths of climbing aroids and cyclanths, and orchids and bromeliads are abundant even near ground level. Many tree trunks are mossy, but the moss is a thin film and does not form thick, wet mats. Tangled vines (including some woody lianas) are common everywhere. The forest floor is thickly littered with leaves, twigs and branches and scattered with fallen logs. There is a thin humus layer over the clay in some places. (R.S. Voss field notes, 1989)

Information regarding the microhabitats of *Heteromys anomalus* near Charlottesville is also available (R.S. Voss and M.E. Holden field notes, 1989). All were captured on the ground in forest (all but four in montane forest). Individual microhabitats follow: under fallen vegetative litter and leaves; under wet vegetative litter and leaves beside tree; under fallen palm fronds; under rotting palm fronds beside large tree; beside rotting log under dead palm frond, fallen branches and other vegetative litter; under log; under inclined tree trunk (2 individuals); under roots of fallen tree; under stilt roots of *Cecropia*; under stilt roots of small tree; under tree ferns and aroids; beside trees under tangled vines; beside buttress of large tree with vine coverage.

CONSERVATION STATUS: *Heteromys anomalus* faces no substantial risk of extinction, but local populations are vulnerable to declines or extirpation in areas undergoing deforestation. Available data indicate that *H. anomalus* inhabits principally closed-canopy forests, but not xerophytic vegetation, natural or anthropogenic grasslands, or large, open agricultural areas (e.g., mechanized agriculture; Utrera et al., 2000). However, in contrast to most species of the genus, it is also known from small plots of subsistence agriculture; see Natural History; see also Anderson, 2003b: 24–25). Furthermore, in addition to evergreen forests typical of the genus, it also inhabits areas where deciduous forests constitute the predominant vegetational type. In such regions, however, it remains unclear whether the species occupies deciduous forests per se, or only smaller areas of evergreen vegetation in more mesic situations, such as along watercourses. The species exhibits a very widespread distribution throughout most of northern Colombia and northern Venezuela, as well as much of Trinidad and Tobago. In central and eastern Venezuela, the species has been collected in many national parks (Parques Nacionales Cerro El Copey-Jóvito Villalba, El Ávila, El Guácharo, Guatopo, Henri Pittier, Miguel José en Sanz San Esteban, and Península de Paria) and other governmentally protected areas (Monumentos Naturales Cerros Matasiete-Guayamurú and Cueva del Guácharo). These reserves receive varying levels of protection; whereas some face substantial human pressure, others (e.g., Parque Nacional Henri Pittier) contain large extents of intact forest.

## DISCUSSION

### BIOGEOGRAPHY OF *HETEROMYS CATOPTERIUS* AND *H. ANOMALUS*

ENDEMISM IN THE CORDILLERA DE LA COSTA: Current information suggests that *Heteromys catopterius* is endemic to the Cordillera de la Costa (figs. 1, 4). Records derive from throughout the Serranía del Litoral, and the species is also known from one area of the Serranía del Interior (near Tiara, in Estado Aragua). Because this latter range is lower and drier, it probably offers much less extensive areas of suitable habitat for the species. *Heteromys catopterius* is not known from mountain ranges to the west of the Cordillera de la Costa. No records of the species exist in the Sierra de Aroa to the west of the Cordillera de la Costa and separated from it by the Depresión de Yaracuy

(SAGCN, 1995). The floral composition of the Sierra de Aroa shows strong similarities to the Cordillera de la Costa (Huber, 1997), but the upper portions of that range have received very little sampling by mammalogists, and conclusions regarding its mammalian fauna must await further fieldwork (see Anderson, 2003a, for methods of testing hypotheses regarding a species' absence). The presence of *H. catopterius* seems much less likely in the Cordillera de Mérida or Serranía de San Luis even farther to the west. Extensive sampling for small nonvolant mammals has occurred in many portions of the Cordillera de Mérida, yielding many records of *H. anomalus* (Anderson, 2003b). The Serranía de San Luis occupies a very isolated position far from other mesic montane regions in northern Venezuela, and available records document the presence of *H. anomalus* there as well (Anderson, 2003b).

Similarly, several mountain ranges present near the eastern end of the known distribution of *Heteromys catopterius* lack records of the species. Two subranges comprise the Macizo Oriental (the easternmost portion of the Cordillera de la Costa). All documented populations of *H. catopterius* in the Macizo Oriental correspond to the Caripe region in the eastern subrange, which is lower and wetter (Huber, 1997). None derive from the higher and drier Cerro Turimiquire subrange just to the west, an area that has received little sampling by mammalogists (Tate, 1931; G.H.H. Tate field notes, 1925). The only specimen of *Heteromys* known from the higher areas on Cerro Turimiquire represents *H. anomalus* (locality 114). Similarly, no records of *H. catopterius* exist from moderately high montane regions on the Península de Paria in extreme northeastern Venezuela, where *H. anomalus* is known, or on Trinidad or Tobago, two continental islands with plentiful records of *H. anomalus*. Interestingly, the habitat of *H. anomalus* at Pigeon Peak in Tobago (see Natural History of *H. anomalus*) holds many similarities with that of sites on the mainland where *H. catopterius* has been collected in large numbers (e.g., Rancho Grande and Hotel Humboldt; see Natural History of *H. catopterius*).

Following current taxonomy, the Cordillera de la Costa harbors only three endemic species of mammals, out of the 327 (Linares, 1998) to 351 (Ochoa-G. and Aguilera-M., 2003) mammals estimated to inhabit Venezuela. An oryzomyine rodent, *Nephelomys caracolus* (formerly included in the *Oryzomys albigularis* species complex) shows a distribution somewhat similar to that of *Heteromys catopterius*, inhabiting the central portion of the Cordillera de la Costa (both the main Aragua-Carabobo chain and the El Ávila massif) at elevations between 1050 and 2300 m; however, in contrast to *H. catopterius*, no records of *N. caracolus* exist from the Serranía del Interior or the Macizo Oriental (Percequillo, 2003; see also Aguilera et al., 1995a; Márquez et al. 2000; Anderson, 2003a). Even more restricted, an ichthyomyine rodent, *Ichthyomys pittieri*, remains known from only a few specimens from the Serranía del Litoral (Handley and Mondolfi, 1963; Voss, 1988). Whereas several species of nonmammalian tetrapods show distributions restricted to montane areas on the Península de Paria in northeastern Venezuela (Estado Sucre) as well as in the Cordillera de la Costa (see below), currently available information indicates that no mammal shows that pattern. Not surprisingly, the mammals endemic to the Cordillera de la Costa are rodents, which typically show small home ranges and low dispersal abilities. Future taxonomic revisions may alter this preliminary information by bringing to light other endemic species currently considered to belong to widespread species (as has happened with revisions of the common rodents *Heteromys* and *Nephelomys*). On the contrary, however, new fieldwork may extend the known ranges of these three species, altering the present conclusions regarding their endemism.

Rates of avian endemism in the Cordillera de la Costa appear grossly similar to the situation in mammals, but estimates range much higher for amphibians and reptiles. Although taxonomic studies and inventory work remain incomplete (especially for amphibians and reptiles), we provide information from available biogeographic summaries of nonmammalian tetrapods (note that regions of endemism in Cracraft [1985] and Péfaur and Rivero [2000] include the surrounding lowlands; therefore, the information provided in those sources cannot be used in the present comparisons of *montane* endemism). Among a total of 1360 species of birds considered to occur in Venezuela, seven or eight are endemic to the Cordillera de la Costa (Lentino-R., 2003); broadening the definition of the region of endemism to include montane areas on the Península de Paria would add five other species. Note, however, that Hilty (2003) indicated more extensive distributions for five of these 13 species, including other montane systems in northern Venezuela, most commonly the Sierra de Aroa and Serranía de San Luis. Of the 284 species of amphibians documented for the country, 27 are endemic to a region including the Cordillera de la Costa and the Península de Paria; information for amphibian endemism in the Cordillera de la Costa itself is not available (La Marca, 2003a). In total, 341 species of reptiles are estimated to inhabit Venezuela, but published information regarding Venezuelan reptiles in the Cordillera de la Costa remains lacking (La Marca, 2003b). Ongoing research indicates that at least 27 species of reptiles are endemic to the Cordillera de la Costa and montane areas on the Península de Paria; at least 20 of those are endemic to the Cordillera de la Costa itself (G. Rivas, in litt.). As is the case for mammals, future fieldwork and taxonomic research may alter these conclusions.

ECOGEOGRAPHY: Although most localities of *Heteromys catopterius* correspond to wet highland sites (including many cloud forests), the species also has been documented at intermediate elevations in sufficiently wet areas. The lowest occurrence record of the species on the southern versant of the main Aragua-Carabobo chain lies at 1050 m (Rancho Grande; locality 137), but the species inhabits wet forests at 680 m elevation on the moister northern slope in Estado Aragua (Carretera Estación Biológica Rancho Grande–Cata, km 29; locality 129) and even as low as 350 m in the Río Morón drainage in Estado Carabobo (La Justa; locality 141; figs. 1, 4). On the El Ávila massif, the species descends to 1050 m on the southern slope along the border between Distrito Captial and Estado Miranda (Quebrada Chacaito; locality 147), but records of the species are known from as low as 720 m on the wetter northern slope (Los Canales de Naiguatá; locality 160; Estado Vargas). These altitudinal patterns coincide with known vegetational differences. Although much local variation exists (related to factors such as exposure to wind), mesic vegetational zones generally descend farther on the northern (Caribbean-facing) slope of the Serranía del Litoral than on the southern, interior versant (Huber, 1997; Ataroff-S., 2003; Meier, 2004).

We conclude that *Heteromys catopterius* has a disjunct distribution within the Cordillera de la Costa. At the very least, the low, dry Depresión de Unare surely isolates the eastern populations in the Macizo Oriental from those in the western and central part of the range of the species. In addition, the central populations on the El Ávila massif may be disjunct from the western populations in the main Aragua-Carabobo chain, due to the drier and moderately low saddle drained by the Quebrada Tacagua on the northwest and the Río Guaire on the southeast (through the city of Caracas). It remains even less clear whether populations in the Serranía del Interior are contiguous with those of the Serranía del Litoral. In any case, the species constitutes a system propitious for fascinating phylogeographic work, especially in a comparative context (i.e., in comparison with other codistributed species, such as *Nephelomys caracolus*) and in conjunction with niche-based distributional modeling in a Geographic Information Systems (GIS) framework (Graham et al., 2004; Phillips et al., 2006).

The ecogeographic patterns of records of *Heteromys anomalus* also merit comment and future research. *Heteromys anomalus* only rarely inhabits localities over 1400 m in regions of the Cordillera de la Costa where *H. catopterius* is present. *Heteromys anomalus* shows a distribution complementary to that of *H. catopterius*, inhabiting higher elevations on the southern (interior) slopes of the central portions of the Cordillera de la Costa than it does on the northern versants. Eight localities above 1000 m exist for *H. anomalus* in the central portion of the Cordillera de la Costa, but none reaches 1400 m (localities 47, 51–53, 62, 63, 75, and 76, Estados Aragua, Carabobo, and Miranda, 1050–1350 m). All pertain to either the southern slopes of main Aragua-Carabobo chain or the Serranía del Interior. In contrast, the highest records of the species on the northern slope of the main Aragua-Carabobo chain and the El Ávila massif are only 920 m and 800 m, respectively (locality 45, Estado Aragua; locality 120, Estado Vargas). In the eastern portion of the Cordillera de la Costa (the Macizo Oriental), *H. anomalus* occurs at elevations above 1000 m at five localities. Four lie in the eastern portion of the Macizo near Caripe and known records of *H. catopterius*, and only one of those corresponds to an elevation above 1400 m (localities 82–84, 86, Estado Monagas, 1060–1550 m). The last is from Cerro Turimiquire at a much higher elevation (locality 114, Estado Sucre, 6000 ft [1829 m]) in the western portion of the Macizo, which is drier (Huber, 1997) and where no record of *H. catopterius* is known.

In contrast to its distribution in the Cordillera de la Costa (where it very rarely exceeds 1400 m), *Heteromys anomalus* is documented from localities above 1400 m in several ranges to the west, outside the range of *H. catopterius*. These include the Sierra Nevada de Santa Marta (San Miguel, Departamento de La Guajira, Colombia, 1700 m), Serranía de Perijá (Sierra Negra, Departamento de la Guajira, Colombia, 1500 m), Serranía de San Luis (Cerro La Danta, Estado Falcón, 1300–1470 m), and Cordillera de Mérida (Cerro Alto, Estado Barinas, 1460–1600 m; El Blanquito and other localities near Sanare, Estado Lara, 1500–1700 m; near Estánquez, Estado Mérida, 1500 m; and near Boconó [in the semi-isolated Macizo de Guaramacal, where several species of mammals show atypically high distributions, Soriano et al., 1990], Estado Trujillo, 2430 m; Anderson, 2003b). Notably, in the isolated Sierra de Aroa between the Cordillera de Mérida and the Cordillera de la Costa, records of *H. anomalus* reach only 800 m (Finca El Jaguar, 680–800 m; Anderson, 2003b). Future fieldwork at higher elevations in that range is likely to discover populations of some species of *Heteromys* in the mesic montane forests there (IGVSB, 2004), which have received very little sampling by mammalogists.

The ecogeographic patterns of *Heteromys catopterius* and *H. anomalus* described above beg for studies assessing the relative importance of climate, biotic interactions, and history in determining their distributions. Likely, all three classes of factors will prove important. Clearly, the localities that the species inhabit differ in climate. In addition, however, occurrence records intimate the possibility of competitive exclusion of *H. anomalus* from some areas of suitable habitat by *H. catopterius*. Finally, the absence of *H. catopterius* from some ranges likely derives from dispersal limitations. To distinguish between these hypotheses in particular regions, niche-based distributional modeling and considerations of sampling adequacy in a GIS framework are needed (e.g., Anderson et al., 2002a, 2002b; Anderson, 2003a; Graham et al., 2004; Phillips et al., 2006).

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NOTE ADDED IN PROOF: After this paper went to press, results of genetic studies by Duke S. Rogers and colleagues prompted us to reexamine specimens from the Guatopo region of the Serranía del Interior in Estado Miranda and Estado Guárico; based on these examinations, we reidentify two specimens as *Heteromys catopterius*, leading to modified biogeographic interpretations. TCWC 39720 (locality 78) and CM 78172 (locality 80) represent *H. catopterius*, but all other specimens from locality 80 correspond to *H. anomalus*. We confirm TTU and USNM specimens from localities 69 and 79 as *H. anomalus*, and our notes for the additional EBRG specimen from locality 69 as well as the MIZA specimen from locality 81 indicate that they match the diagnosis of *H. anomalus* as well. Many of these specimens constitute vouchers from important ecological, karyological, and genetic research, some of which should be reinterpreted based on these findings. Although the two vouchers for the copious ecological and natural history information provided by O'Connell (1981; see also Eisenberg et al., 1979) are both *H. anomalus* (locality 79), published phenetic and phylogenetic analyses based on allozymic data include specimens of both *H. catopterius* and *H. anomalus* from localities 78 and 80 (Rogers, 1990; Anderson et al., 2006; D. S. Rogers, in litt.). It remains unclear whether any of the standard karyotypes for Venezuelan *Heteromys* reported by Engstrom et al. (1987) derives from the lone specimen of *H. catopterius* from locality 80.

The discovery of *Heteromys catopterius* in this region holds several biogeographic implications. First of all, these specimens represent an extension of the known range of the species within the Serranía del Interior ca. 70 km to the east. Here, *H. catopterius* is now documented from 400 m and 526 m on the northern slope of the Serranía del Interior (localities 78 and 80) and is sympatric with *H. anomalus* at the latter site (where habitat information for the two species is not available, unfortunately). In contrast, *H. anomalus* occurs at slightly higher elevations near the crest of the range on both the northern (710 m; 600–800 m; localities 79 and 81) and southern (680–720 m; locality 69) versants. Although with so few records it is not possible to characterize the species' distributions in the region in detail at present, they may coincide with local climatic differences and/or levels of habitat disturbance, as in other parts of their ranges. Notably, the northern faces of the coastal ranges, such as where *H. catopterius* has been collected at Guatopo, generally are wetter than the southern ones (Eisenberg et al., 1979; Huber, 1997; Ataroff-S., 2003; Meier, 2004). Presumably, *H. anomalus* also inhabits lower, slightly drier areas in the surrounding lowlands (e.g., locality 77, 50–70 m), but no nearby record of either species exists below 400 m.

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# APPENDIX 1

## Gazetteer and Specimens Examined in Principal Study Area

Here we report all specimens of *Heteromys* examined from central and eastern Venezuela (east of the Depresión de Yaracuy that separates the Cordillera de Mérida and Sierra de Aroa from the Cordillera de la Costa) and from Trinidad and Tobago (see Museum Specimens). Secondary information deriving from sources other than the collector is included in brackets and, where applicable, is followed by the source. Where original elevation was reported in feet, we provide that datum as well as the metric equivalent to the nearest whole number. Localities are numbered to correspond to figure 4, where they are plotted, and are arranged from north to south within states in Venezuela or major island in Trinidad and Tobago. For each entry, boldface type indicates the place name to which geographic coordinates correspond. We estimate that most coordinates are accurate to within 5 km (ca. 2 minutes); the placement of "ca." immediately before the coordinates indicates those accurate to an estimated 6–10 km. Museum catalog numbers for specimens examined follow each locality, using the abbreviations provided in Materials and Methods. Early specimens in the AMNH and USNM for which the osteological portion was cataloged in a separate numbering sequence from the skin are indicated as skin number/osteological number. See appendix 2 for specimens examined outside the principal study area.

### *Heteromys anomalus* (total 993)
### TRINIDAD AND TOBAGO (total 453)

### Tobago

1. St. John Parish, **2.5 km SSW Charlottesville, Pigeon Peak**, Tobago Forest Reserve, 550 m, 11°18′N, 60°33′W, USNM 540705–540708; St. John Parish, **Charlottesville, 2.5 km SW [SSW], Pigeon Peak**, Tobago Forest Reserve, 550 m, 11°18′N, 60°33′W, USNM 540641–540643; St. John Parish, **Pigeon Peak**, 335–570 m [same coordinates; O. S., 1926; Goodwin and Greenhall, 1961; Voss, 1991], USNM 540721, 540722; and near Charllottesville [near **Pigeon Peak**; ca. 200–520 m; same coordinates; R.S. Voss field notes, 1989; Voss, 1991], AMNH 259985–259997.
2. **Spey Side** [= Speyside; ca. 0–300 ft (0–91 m); 11°18′N, 60°32′W; O. S., 1926; Voss, 1991; not Goodwin and Greenhall, 1961], AMNH 184785.
3. **1.5 km S Pigeon's Peak** [ca. 800–1400 ft (244–427 m); 11°17′N, 60°33′W; O. S., 1926], USNM 538072.
4. St. Paul Parish, 4.5 km N Roxborough, **Roxborough Valley** and Ranch [< 1000 ft (305 m); 11°16′N, 60°35′W; displacement north of Roxborough likely road distance; coordinates correspond to midway point of Roxborough River at ca. 250 ft (76 m); O. S., 1926], USNM 540709, 540710.

### Trinidad

5. **Caura** [600 ft (183 m); 10°43′N, 61°21′W; O. S., 1930; Goodwin and Greenhall, 1961; Voss, 1991], AMNH 7523, 7524, 7567/5960, 7568/5961, 7569/5962, 7570/5988, 7572/5964, 7573/5965, 7574/5966, 7575/5967, 7578/5970, 7579/5971, 7580/5972, 7581/5973, 7583/5975, 7584/5976, 7586, 7587/5978, 7588/5979, 7589/5980, 7590/5981, 7591/5982, 7592/5983, 7594/5985, 7596/5987, 7597, 7598/5989; BM(NH) 97.4.5.1 (= AMNH 7577/5969), 97.4.5.2 (= AMNH 7582/5974); MCZ B7775 (= AMNH 7593/5984), B7776; USNM 85570 (= AMNH 7585/5977); and St. George County, Tacarigua Ward, **Caura**, 600 ft [183 m; same coordinates], FMNH 5373, 5375.
6. N[orth] Ranges, **Guacharo Cave**, Aripo [= Aripo Cave; "about 3 miles (5 km) from the Aripo Valley Road"; Goodwin and Greenhall, 1961: 293; 2700 ft (823 m); 10°43′N, 61°15′W; coordinates correspond to indicated elevation on Cerro de Aripo, ca. 3 km NW of end of Aripo Road; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], BM(NH) 33.12.4.8.
7. **Cumaca** [1200 ft (366 m); 10°42′N, 61°10′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 169704, 169717, 169727, 169738, 169739, 169768, 214451.
8. **St. Anne's Valley** [drained by St. Ann's River, which leads to populated area of same name on northeastern outskirts of Port-of-Spain; < 2000 ft (610 m); 10°41′N, 61°30′W; precise location in valley not available; coordinates correspond to midway point of St. Ann's River; O. S., 1930; Goodwin and Greenhall, 1961], USNM 21031/A36071.
9. Behind **St. Ann's** barracks; high road, close by **St. Anne's** barracks [suburb northeast of Port-of-Spain; ca. 200 ft (61 m); 10°40′N, 61°31′W; O. S., 1930; Goodwin and Greenhall, 1961], BM(NH) uncataloged "12.a" (holotype of *Mus anomalus*); and Botanic Gardens [= Royal Botanic Gardens; **North District, Port-of-Spain**; Goodwin and Greenhall, 1961; < 200 ft (61 m); same coordinates; O. S., 1930], BM(NH) 91.7.2.1, 92.9.7.10.
10. **Rio Grande**, near Tree Station [= Rio Grande Forest; 200 ft (61 m), 10°40′N, 61°05′W; O. S., 1930; Goodwin and Greenhall, 1961; not Voss, 1991], AMNH 174072; and **Rio Grande Forest**, Sangre Grande [same coordinates], AMNH 174073–174075.
11. **Matura** [150 ft (46 m); 10°40′N, 61°04′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 174070.
12. St. Pats [near **Arima**; 100 ft (30 m); 10°38′N, 61°17′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 169675, 169678, 169687; and St.

Pats, **Arima** [same coordinates], AMNH 169674, 169682.

13. **Ravine Sable** Trace, Vega de Oropouche [50 ft (15 m) for Vega de Oropuche; 10°37′N, 61°04′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 186467.
14. Cornelliac Estate, **Vega de Oropouche** [50 ft (15 m); 10°36′N, 61°05′W; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 188406; La Fortune Estate, **Vega de Oropouche** [same coordinates], AMNH 186468–186470; St. Andrew, **Oropuche [= Vega de Oropuche],** La Fortune Estate [same coordinates], UF 6571, 6572; and **Vega de Oropouche** [same coordinates], AMNH 186466.
15. **Cumuto** [100 ft (30 m); 10°35′N, 61°12′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 209004, 209005, 212306–212308.
16. **Sangre Grande** [100 ft (30 m); 10°35′N, 61°07′W; O. S., 1930; Goodwin and Greenhall, 1961; Voss, 1991], AMNH 174071; Maingot Estate, 5 miles [8 km] from **Sangre Grande** [ca. 10°35′N, 61°07′W; O. S., 1930; Voss, 1991], AMNH 174077–174088, 174091–174094, 174246–174248; and Maingot Estate, **Sangre Grande** [same coordinates], AMNH 174076, 174089, 174090, 186465.
17. **Fishing Pond** [< 100 ft (30 m); 10°35′N, 61°03′W; O. S., 1930], AMNH 174069.
18. St. George County, San Rafael Ward, **San Rafael**, 100 ft [30 m; 10°34′N, 61°16′W; O. S., 1930], FMNH 62050.
19. **North Manzanilla** [50 ft (15 m); 10°32′N, 61°01′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 186446–186449.
20. **Manzanilla** [100–200 ft (30–61 m); 10°31′N, 61°04′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 186471.
21. **Caparo** [150 ft (46 m); 10°27′N, 61°19′W; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 7522, 7562/5955, 7563/5956, 7564/5957, 7565/5958, 7566/5959, 22862.
22. **Bush Bush Forest**, Nariva Swamp [ca. sea level; 10°24′N, 61°03′W; O. S., 1930; Downs et al., 1968], AMNH 185471, 186626–186672, 186673 (skull 188377), 186674 (skull 188378), 186676 (skull 188379), 186677 (skull 186675), 186678–186713, 186714 (skull 188395), 186715, 186716 (skull 188396), 186717–186723, 186724 (skull 186726), 186725, 186727 (skull 188398), 186728 (skull 188399), 186729 (skull 188400), 186730 (skull 188402), 186731 (skull 188403), 188366, 188367, 188369–188376, 188380–188387, 188390–188394, 188397, 188401, 188404, 188405, 212136; **Bush Bush** [= Bush Bush Forest], Nariva Swamp [same coordinates], UF 6573; **Bush Bush** [= Bush Bush Forest; same coordinates], AMNH 203075–203079, 203081–203085, 203087–203101, 203103–203113, 204750, 204751, 204753–204763, 204765–204775, 204858–204879, 206598–206603, 206769–206775; and **Bush Bush Forest** [same coordinates], AMNH 186450–186464, 189318–189322, 235007–235009.
23. Victoria County, **Brickfield** [ca. 100–200 ft (30–61 m); 10°20′N, 61°16′W; O. S., 1930], FMNH 61899–61902.
24. **Mayaro** ["14 miles (23 km) east of Rio Claro on the Naparima–Mayaro Road at the 39-mile post"; Goodwin and Greenhall, 1961: 294; 50 ft (15 m); 10°18′N, 61°01′W; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 235012–235014.
25. Princestown [= **Princes Town**; 100–150 ft (30–46 m); 10°16′N, 61°23′W; Anonymous, unknown year; O. S., 1930; Goodwin and Greenhall, 1961], AMNH 1615–1619; Princestown [= **Princes Town**; same coordinates], AMNH 6003–6007, 6010–6017, 6021–6027; unmatched skull numbers AMNH 4730–4732, 4735–4742, 4746–4752; MCZ 27040 (= AMNH 7576/5968); USNM 85568 (= AMNH 6008/4733), 85569 (= AMNH 6019/4744); and St. George County, Savana Grande Ward, Princestown [= **Princes Town**; same coordinates], FMNH 5374, 5376.
26. **Cedros** [< 200 ft (61 m); O. S., 1930; precise location in Cedros Ward unavailable; approximate center of Ward has coordinates ca. 10°06′N, 61°48′W; Goodwin and Greenhall, 1961], AMNH 235010, 235011.
27. **Hollis Reserve** [not located; but note a Hollis Reservoir present at ca. 10°42′N, 61°11′W; Anonymous, unknown year], BM(NH) 95.22.
28. **Little Swamp, Cedros** [< 200 ft (61 m); O. S., 1930; not located; approximate center of Cedros Ward has coordinates ca. 10°06′N, 61°48′W; Goodwin and Greenhall, 1961], AMNH 235018.
29. **Lokano** [not located], BM(NH) 97.6.7.10.
30. **Turure Forest** [not located; but note Turure Ward, with approximate center at 10°32′N, 61°07′W; Goodwin and Greenhall, 1961], AMNH 235015–235017.

–. no specific locality, AMNH 204880, BM(NH) 37.11.11.5, 37.11.11.6, 37.11.11.7, 95.3.9.4.

## VENEZUELA (total 540)

### ANZOÁTEGUI

31. **Pekín** Abajo, Río Neverí, 100 m [10°09′N, 64°31′W; DCN, 1972b], MHNLS 1395, 1421.
32. **Hato Capacho**, 2 km S [ca. 8 km ESE] de Urica [ca. 280 m; ca. 9°41′N, 63°56′W; DCN, 1968b], EBRG 21732.
33. Sabana de Río Caris, Hacienda **San Antonio** [ca. 160 m; 8°37′N, 64°04′W; DCN, 1966], MBUCV I-4740, 4741.
34. Río Caris, Paso **Los Cocos**, 280 m [ca. 120 m; DCN, 1966; 8°36′N, 64°04′W; S. Boher, in litt.; DCN, 1966; not Voss, 1991], MBUCV I-4745; Paso **Los Cocos**, Río Caris [same coordinates], MBUCV I-3121–3125; Paso **Los Cocos**, Río Caris, S El Tigre [same coordinates], MBUCV I-3496; and Río Caris, SE de Paso **Los Cocos** [same coordinates], MBUCV I-4744.
35. Río Caris, **Morichal Temblador** [tributary of the Río Hamaca, which is a tributary of the Río Pao, ca. 30 km W of the Río Caris; ca. 140–160

m; 8°34′N, 64°23′W; DCN, 1966], MBUCV I-4746.

36. Guayabal, **Hacienda San Antonio** [paso entre Guayabal y Los Tablones; S. Boher, in litt.], Río Pao, 100 m [8°31′N, 64°27′W; DCN, 1966; not Voss, 1991], MBUCV I-3126, 3127, 4742.
37. Río Caris, **La Ceiba** [not located; may be the site La Ceiba at ca. 80 m and 8°20′N, 63°59′W on Morichal La Ceiba, a tributary of the Río Limo, ca. 20 km W of the Río Caris; DCN, 1971d], MBUCV I-4747.
38. **Río Pao** [precise location along river not available], MBUCV I-4743.

## ARAGUA

39. **Cumbre de Turiamo** [= Cerro La Cumbre; ca. 400 m; 10°26′N, 67°48′W; DCN, 1971b], EBRG 359, 360.
40. **3 km S Ocumare [de la Costa]**, sea level [10°26′N, 67°46′W; DCN, 1971b], USNM 517542.
41. Carretera Estación Biológica Rancho Grande–Cata, **La Trilla**, 50 m [10°24′N, 67°45′W; DCN, 1971b; Paynter, 1982], MIZA 20-273, 20-278; **La Trilla**, lado norte, Maracay, 50 m [same coordinates], MIZA 20-441; **La Trilla**, Parque Nacional Henri Pittier [same coordinates], MIZA 20-440; **La Trilla**, vía Ocumare [de la Costa]–Maracay, 50 m [same coordinates], MIZA 20-439; **La Trilla**, vía Ocumare [de la Costa]–Maracay, lado norte, 50 m [same coordinates], MIZA 20-437; and Vía Maracay–Cata, **La Trilla** [same coordinates], MIZA 20-274.
42. **Carretera Ocumare de la Costa, cerca a Ocumare**, 250 m [10°23′N, 67°45′W; coordinates correspond to indicated elevation near Ocumare de la Costa; DCN, 1971b], MIZA 20-223.
43. **Carretera Estación Biológica Rancho Grande–Cata, km 36**, Parque Nacional Henri Pittier, 300 m [10°23′N, 67°44′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-277, 20-283; **Carretera Ocumare de la Costa**, Parque Nacional Henri Pittier, 250 m [same coordinates], MIZA 20-228; and **Km 36, vía Ocumare [de la Costa]–Maracay**, lado norte [same coordinates], MIZA 20-438.
44. **Carretera de Ocumare [de la Costa], ladera norte**, 630 m [10°22′N, 67°44′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-342; and **Vía Ocumare de la Costa**, lado norte, 500 m [same coordinates], MIZA 20-224. See also locality 129 for specimens of *H. catopterius* from the same locality.
45. **Carretera de Ocumare [de la Costa], lado norte**, 920 m [10°22′N, 67°42′W; Beebe and Crane, 1947: 48; DCN, 1971b], MIZA 20-346; and **Carretera Estación Biológica Rancho Grande–Cata, km 24**, Parque Nacional Henri Pittier [900 m; see locality 130; same coordinates], MIZA 20-279. See also locality 130 for specimens of *H. catopterius* from the same locality.
46. **Vía Ocumare de la Costa** [N slope, R. Visbal, personal commun.], 695–750 m [10°21′N, 67°43′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-227, 20-395.
47. **Estación Biológica Rancho Grande**, 13 km NW Maracay, 1050 m [10°21′N, 67°40′W; DCN, 1971b; Handley, 1976; but see Paynter, 1982], EBRG 15047–15049; and **Rancho Grande** [same coordinates], AMNH 144411. See also locality 137 for specimens of *H. catopterius* from the same locality.
48. Parque Nacional Henri Pittier, **4.6 km by road S Rancho Grande**, 750 m [10°20′N, 67°39′W; DCN, 1971b], EBRG 16955.
49. **Estación de Piscicultura** [= current Museo de la Estación Biológica Rancho Grande], El Limón [ca. 500 m; 10°19′N, 67°39′W; J. Sánchez-H., personal commun.; DCN, 1991], EBRG 131–133; **Estación Piscicultura** [= current Museo de la Estación Biológica Rancho Grande], El Limón, Maracay [same coordinates], EBRG 188; and Parque Nacional Henri Pittier, **Estación Piscicultura MAC** [Ministerio de Agricultura y Cría; = current Museo de la Estación Biológica Rancho Grande], El Limón [same coordinates], MIZA 20-004.
50. **El Limón**, 4 km NW Maracay, 524 m [10°18′N, 67°38′W; Paynter, 1982], USNM 517544.
51. **La Horqueta**, vía a Tiara, 1100 m [10°12′N, 67°08′W; DCN, 1972a], MBUCV I-1554, 1555.
52. **Agua Amarilla**, carretera a Tiara [ca. 1080 m; 10°11′N, 67°08′W; DCN, 1972a], MHNLS 454.
53. **Campamento Rafael Rangel** [Sierra Maestra; Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.], 1260 m [10°09′N, 67°09′W; DCN, 1972a; not Voss, 1992; or Adams and Lewis, 1995], USNM 317697–317699, 317701, 317703, 317705–317707, 317709, 317710; and **Campamento Rangel** [Sierra Maestra; Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.; same coordinates], USNM 314817. See also locality 138 for specimens of *H. catopterius* from the same locality.
54. **Carretera a Tiara** [precise location along road from La Victoria to Tiara not available; Tiara has coordinates of 10°08′N, 67°09′W; DCN, 1972a], MHNLS 1192–1194.

## CARABOBO

55. **Río Abajo**, 10 km [W] de Morón [< 40 m; 10°29′N, 68°17′W; DCN, 1983], MBUCV I-4252; and **Río Abajo**, 10 km SW [W] de Morón [same coordinates], MBUCV I-4099.
56. **Agropecuaria Yapascua**, Ensenada Yapascua, E de Patanemo, 0 m [10°27′N, 67°54′W; J. Sánchez-H., personal commun.; DCN, 1971b], EBRG 8192; and **Agropecuaria Yapascua, Quebrada Yapascua**, al E de Patanemo, 50 m [same coordinates], EBRG 8171, 8193–8195.
57. Hacienda Saint Jean, **2 km SW de Borburata**, 40 m [10°26′N, 67°58′W; DCN, 1971b], EBRG 8167; and Hacienda Saint Jean, Borburata [= **2 km SW de Borburata**], 40 m [same coordinates], MHNLS 7351.

58. Bahía de **Patanemo**, 50 m [10°26′N, 67°55′W; DCN, 1971b], MHNLS 3737; and **Patanemo**, 10 m [same coordinates], MHNLS 3736, 3738, 3739.
59. **San Esteban**, northern Venezuela, 1500 ft [457 m; ca. 10°25′N, 68°01′W; coordinates correspond to indicated elevation SW (above) San Esteban; DCN, 1983; see also Phelps, 1944; Paynter, 1982], BM(NH) 11.5.25.149, 11.5.25.150; and **San Esteban**, northern Venezuela, hills, 1800 ft [549 m; same coordinates], BM(NH) 11.5.25.151.
60. **Las Quiguas** [650 ft (198 m); 10°24′N, 68°00′W; Allen, 1911; Paynter, 1982; DCN, 1971b; DCN, 1983], AMNH 31544, 31545.
61. Hacienda Saint Jean, **13 km [by road] SW de Borburata**, 120 m [10°24′N, 67°59′W; DCN, 1983; not Voss, 1991], EBRG 8186.
62. Fila la Josefina, **11 km [by road] NW Tronconero**, 1350 m [10°20′N, 67°55′W; J. Ochoa-G. and J. Sánchez-H., personal commun.; DCN, 1971b; DCN, 1991], MHNLS 7558, 7595; and Fila la Josefina, **11 km NW de Tronconero por carretera**, 1350 m [same coordinates], EBRG 10174, 10146, 10202.
63. La Florida, **Sierra Lorenzo de Bárbula**, 1050–1100 m [10°16′N, 68°03′W; coordinates correspond to indicated elevation SW of Bárbula, W of Naguanagua; DCN, 1975b; DCN, 1976a; DCN, 1976c; not Voss, 1992], MHNLS 2390, 2737.
64. Finca Cujigacho, **Guacara** [ca. 500 m; ca. 10°14′N, 67°52′W; DCN, 1991], MIZA 20-046.
65. 4.5 km SE Montalbán, **Sabana Aguirre**, 1055 m [correct elevation 562 m; A.L. Tuttle field notes, 1967; 10°11′N, 68°18′W; A.L. Tuttle field notes, 1967; DCN, 1976c; but see Handley, 1976], USNM 442100.

## COJEDES

66. **Caño Hondo** [ca. 100–120 m; 9°32′N, 68°40′W; DCN, 1976b], TCWC 55661, 55662.
67. Hato El **Tirado** [ca. 100 m; 9°05′N, 68°25′W; DCN, 1963; not Voss, 1992], MHNLS 3892–3894.
68. **Hato Itabana** [38 km SE Las Vegas, Voss, 1991, 1992], 80 m [not located; unknown whether displacement from Las Vegas is airline or by road; not Voss, 1991, 1992, who gave coordinates for Las Vegas], MHNLS 4406.

## GUÁRICO

69. **50 km S and 39 km E Caracas**, near Guatopo National Park [= 15 km NW Alta Gracia, USNM archives; see also Handley, 1976], 680–720 m [10°01′N, 66°26′W; N.E. Peterson field notes, 1966; DCN, 1970b; see also Handley, 1976], EBRG 15075; USNM 387824–387827.
70. 23 km NE Calabozo, **Hato Los Leones**, Caño Agua Fría, 88 m [correct elevation 150 m; Handley, 1976; 9°03′N, 67°16′W; Handley, 1976], USNM 387822.
71. **Laguna Los Patos**, Estación Biológica los Llanos, Calabozo, 100 m [8°50′N, 67°22′W; DCN, 1970a; see also Handley, 1976], MBUCV I-1856.
72. **Hato Flores Moradas**, 50 km [by road] S Calabozo [ca. 60–75 m; 8°34′N, 67°33′W; DCN, 1971a; not Paynter, 1982], UF 23863.
73. **45 km [by road] S Calabozo** [= Fundo Pecuario Masaguaral; ca. 75 m; 8°34′N, 67°32′W; coordinates correspond to the two deciduous forest grids near Caño Caracol where *Heteromys* was captured; August, 1984; DCN, 1971a], TTU 33445.

## MIRANDA

74. La Toma Capaya, **Río Marasmita**, 250 m [10° 28′N, 66°17′W; coordinates correspond to indicated elevation on Río Marasmita; DCN, 1970c], MHNLS 1791.
75. Valle de Sartenejas, **Universidad Simón Bolívar**, bosquecillo [ca. 1100 m; 10°25′N, 66°53′W; E. Pannier, personal commun.; DCN, 1964a; Aguilera et al., 1995b], MCNUSB I-414.
76. **8 km S Caracas, near Turgua** [= San Andrés, 16 km SSE Caracas; Handley, 1976], 1144 m [10°22′N, 66°50′W; Handley, 1976], USNM 387818.
77. **Estación Experimental Río Negro**, USR [Universidad Nacional Experimental Simón Rodríguez], 50–70 m [ca. 10°20′N, 66°17′W; DCN, 1970b; Ventura et al., 2002], MBUCV I-3633, 3634, 3636, 3637, 3639, 3641, 3684, 4021; **Estación Experimental Río Negro**, USR [Universidad Nacional Experimental Simón Rodríguez], a 30 km [by road] de Caucagua [same coordinates], MBUCV I-4129, 4130, 4188, 4206, 4251; **Estación Experimental Río Negro** [same coordinates], MBUCV I-3149; and **Estación Experimental Río Negro**, 20 km E Caucagua [same coordinates], MCNUSB I-822, 825, 1150.
78. **40 km [by road] N Altagracia** [de Orituco; near Agua Blanca; ca. 400 m; 10°04′N, 66°28′W; J.W. Sites, Jr. field notes, 1980; DCN, 1970b], TCWC 39720.
79. Parque Nacional Guatopo, **24 km N Altagracia** [710 m; 10°03′N, 66°26′W; coordinates correspond to the grid at the southern end of the park where *Heteromys* was captured; P.V. August, in litt.; O'Connell, 1981; not Paynter, 1982; or Musser et al., 1998], TTU 33446; and Parque Nacional Guatopo, by office [**24 km N Altagracia**; P.V. August, in litt.; same coordinates], TTU 35996.
80. **25 km [by road] N Altagracia de Orituco** [Parque Nacional Guatopo, near headquarters; ca. 526 m; 10°02′N, 66°27′W; J.W. Sites, Jr. field notes, 1980; DCN, 1970b], CM 78170–78173; TCWC 39719.
81. Parque Nacional Guatopo, **El Lucero** [ca. 600–800 m; 10°01′N, 66°27′W; DCN, 1970b], MIZA 20-037.

### MONAGAS

82. **Cinco Cruces**, Distrito Caripe, 1100 m [10°16′N, 63°27′W; DCN, 1969b], MBUCV I-289.
83. **Cerro Espejo**, Distrito Caripe, 1550 m [10°11′N, 63°33′W; a Cerro Espejo exists along the Fila Macanillal ca. 15 km SE of Caripe but only reaches ca. 1200 m; coordinates given here correspond to indicated elevation along the Quebrada El Espejo, which drains the northen slope of a small mountain 3 km NW of Caripe and near other localities known for this collector (J. Ojasti); DCN, 1964c; DCN, 1964d], MBUCV I-291, 292.
84. **2 km N and 4 km W Caripe, La Laguna** [= 5 km NW Caripe; Handley, 1976], 1330 m [10°11′N, 63°32′W; N.E. Peterson field notes, 1967; DCN, 1964c; but see Handley, 1976], USNM 409819; and **2 km N and 4 km W Caripe**, near San Agustín [= 5 km NW Caripe; Handley, 1976], 1180–1260 m [same coordinates], USNM 409815, 409816. See also locality 159 for specimens of *H. catopterius* from the same locality.
85. **Campo Allegre** [= Campo Alegre; ca. 600 m; 10°10′N, 63°43′W; a Campo Alegre exists in Estado Sucre ca. 10 km S of Cumaná (note locality 102); coordinates given here correspond to the Campo Alegre present in Estado Monagas (SE of the border with Estado Sucre) near San Antonio, as indicated in early reports of work by this collector (F.W. Urich); DCN, 1964c; Chapman, 1899; not Paynter, 1982], AMNH 14780.
86. **Cueva del Guácharo**, 1060 m [10°10′N, 63°33′W; DCN, 1964c; Aguilera et al., 1995b; not Handley, 1976], MBUCV I-281–287, 290; **Cueva del Guácharo**, Caripe, 1060 m [same coordinates], MBUCV I-288; **Cueva del Guácharo**, Caripe, 1065 m [same coordinates], MHNLS 1102–1104; **Cueva Guácharo** [same coordinates], MHNLS 807, 808; and 5 km W Caripe, **Cueva del Guácharo**, 1010 m [same coordinates], USNM 409820, 409821 (provisional identifications only for USNM 409820 and 409821; see Sympatry and Zones of Contact with *Heteromys anomalus*).
87. **Caripito** [ca. 20–80 m; 10°08′N, 63°06′W; DCN, 1969b; Paynter, 1982], AMNH 142630, 142631, 142633–142640; and **Caripito**, Wotr Camp [same coordinates], AMNH 142629.
88. Caripito [**road between Caripito and dock on Río San Juan**; J.W. Bickham field notes, 1980; < 20 m; 10°08′N, 63°04′W; DCN, 1969b], CM 78161–78163; TCWC 39712, 39713.
89. **San Antonio** [= San Antonio de Maturín], 1500–1800 ft [457–549 m; 10°07′N, 63°43′W; DCN, 1964c; Paynter, 1982], AMNH 69679–69693.
90. **Río Queregua**, Finca Doña Nar, 3 km W [SSW] El Tejero [ca. 200–280 m; ca. 9°37′N, 63°41′W; coordinates correspond to midpoint of the short Río Queregua, ca. 3 km SSW of El Tejero; DCN, 1968a], EBRG 22454, 22455.

### NUEVA ESPARTA

91. **2 km N and 2 km E La Asunción, Cerro Matasiete** [= 3 km NE La Asunción, Handley, 1976], 405 m [11°03′N, 63°51′W; DCN, 1979b; see also Handley, 1976], EBRG 15081; **2 km N and 2 km E La Asunción** [= **Cerro Matasiete**, 3 km NE La Asunción, Handley, 1976], 420 m [same coordinates], USNM 405982; and **3 km N and 2 km E La Asunción, Cerro Matasiete** [= 4 km NE La Asunción, Handley, 1976], 100 m [same coordinates], USNM 405981.
92. **Cerro Copey**, San Juan, 800 m [11°01′N, 63°54′W; DCN, 1979b; but see Paynter, 1982], MHNLS 199.

### SUCRE

93. **Guarataro**, 8 km [by road] E San Juan de las Galdonas [ca. sea level; 10°43′N, 62°48′W; DCN, 1974a], MCNUSB I-1362.
94. **Playa Colorada, Guacuco**, Paria, 0–50 m [10°42′N, 62°50′W; DCN, 1974a], MHNLS 6982, 6984, 6986–6989, 6994; and **Quebrada Colorada, Guacuco**, Paria, 50 m [same coordinates], MHNLS 6934.
95. **10 km N and 5 km E Güiria, near El Mango** [= 11 km NE Güiria, Handley, 1976], 35–45 m [10°40′N, 62°15′W; DCN, 1974b; not Handley, 1976], EBRG 15085; USNM 409810.
96. **Cristobal Colón** [= Macuro], 1500 ft [457 m; 10°40′N, 61°58′W; coordinates correspond to indicated elevation above Macuro; DCN, 1974c; not Paynter, 1982], AMNH 36194–36196.
97. Distrito Valdez, población de **Macuro**, zona del balcón, vaquera, 50 m [10°40′N, 61°57′W; DCN, 1974c], MIZA 20-086; **Macuro**, Península de Paria [same coordinates], MIZA 20-055; and Población de **Macuro**, camino a la antena, el bebedero, 100 m [same coordinates], MIZA 20-087.
98. Entre Caricao y Chacopata [**carretera Cariaco–Chacopata, entre Chacopata y la Quebrada El Corral**, C. Ibáñez, in litt.; ca. sea level; ca. 10°39′N, 63°43′W; DCN, 1970d], MHNLS 6670.
99. **8 km N and 5 km E Güiria, Hacienda La Concordia** [= 9 km NE Güiria; Handley, 1976], 7 m [10°38′N, 62°15′W; Handley, 1976], USNM 409812; and **Ensenada Cauranta**, 9 km NE Güiria, 7 m [same coordinates], USNM 495294.
100. **26 km ESE Carúpano, Manacal**, 180–575 m [10°37′N, 63°01′W; Handley, 1976], EBRG 16683–16690; **4 km S and 25 km E Carúpano, near Manacal** [= 26 km ESE Carúpano; Handley, 1976], 180–300 m [same coordinates], USNM 409849–409851; **5 km S and 24 km E Carúpano, Manacal** [= 26 km ESE Carúpano, Handley, 1976], 600 m [same coordinates], USNM 409839; **5 km S and 25 km E Carúpano** [= 26 km ESE Carúpano, Handley, 1976; same coordinates], EBRG 15092, 15098; **5 km S and 25 km E Carúpano, Manacal** [= 26 km ESE Carúpano, Handley, 1976], 180–600 m [same coordinates],

USNM 409826–409831, 409834, 409835, 409837, 409838, 409841–409843, 409845, 409846, 409848, 409852 , 409854; **5 km S and 25 km E Carúpano, near Manacal** [= 26 km ESE Carúpano, Handley, 1976], 185–600 m [same coordinates], EBRG 15089, 15091, 15093–15097; and **Manacal, 26 km ESE Carúpano**, 175–575 m [same coordinates], USNM 495296–495301, 495303, 495305, 495310, 495313–495319.

101. **Finca Vuelta Larga**, 9.7 km (by road) SE Guaraunos, 10 m [10°30′N, 63°07′W; DCN, 1969c; not Voss 1991, 1992], AMNH 257213–257218, 257222; MHNLS 8118, 8120, 8163, 8172; and **Finca Vuelta Larga**, 9.7 km [by road] SE Guaraúnos [same coordinates], MHNLS 8165, 8166, 8173, 8175.

102. Cumaná, **Campo Alegre**, 1350–1550 ft [411–472 m; 10°22′N, 64°12′W; a Campo Alegre exists at ca. 600 m in Estado Monagas near the border with Estado Sucre ca. 60 km SE of Caripe (note locality 85); coordinates given here correspond to indicated elevation at the Campo Alegre present ca. 10 km S of Cumaná near other localities known for this collector (E. André); DCN, 1964b; not Paynter, 1982], BM(NH) 0.5.1.42, 0.5.1.43, 0.5.1.44.

103. Cumaná, **Ipuré**, 2250 ft [686 m; ca. 10°22′N, 64°08′W; coordinates correspond to highest elevation (ca. 400 m) above town of Los Ipures; DCN, 1964b], BM(NH) 0.5.1.47, 0.5.1.48.

104. **40 km [by road] NW Caripito** [in hills near road marker km 81, ca. 36 km by road N of Río Caripe; J.W. Bickham field notes, 1980; ca. 40–200 m; 10°20′N, 63°20′W; DCN, 1969b, 1969c; ITMB, 2000; not Voss, 1992], CM 78164–78169; TCWC 39714–39718.

105. Cumaná, **Quebrada Secca** [= Quebrada Seca; = Villarroel; ca. 200 m; 10°18′N, 63°57′W; DCN, 1964c; see also Paynter, 1982], BM(NH) 0.5.1.49; **Quebrada Secca** [= Quebrada Seca; = Villarroel; same coordinates], AMNH 14759–14761, 14776–14779.

106. **Cumanacoa**, 700 ft [213 m; 10°15′N, 63°55′W; DCN, 1964c; Paynter, 1982], AMNH 69694–69696.

107. **Paujucillo**, Santa María de Cariaco [ca. 800 m; 10°15′N, 63°35′W; DCN, 1964c], MCNUSB I-768, 769.

108. **Cuchivano** ["at the foot of the slope on the southwest side of the valley a few miles from Cumanacoa" near Quebrada Juajua = Río Guasdua; Tate, 1931: 540], 700 ft [213 m; 10°14′N, 63°56′W; DCN, 1964c, unknown year b], AMNH 69647, 69648.

109. Los Palmales [near San Antonio, Santa Ana valley, **Los Dos Ríos**; 450 m; Wetmore, 1939; ca. 10°13′N, 63°52′W; DCN, 1964c; not Paynter, 1982; contra placement of Los Palmales in Estado Monagas by Phelps, 1944: 416–417], AMNH 14750–14758, 14762–14775.

110. Quebrada Yoraco, cerca de **Las Trincheras**, base Cerro Turimiquire [ca. 400 m; 10°12′N, 63°55′W; DCN, 1964c], EBRG 8196.

111. **Neverí**, 2400 ft [732 m; 10°11′N, 64°05′W; coordinates correspond to indicated elevation along Río Neverí; G.H.H. Tate field notes, 1925; DCN, 1969a; not Paynter, 1982; or Voss, 1988], AMNH 69649–69673.

112. **Cocollar** [= Cocoyar], 2600 ft [792 m; 10°11′N, 63°49′W; DCN, 1964c; see also Tate, 1931; not Paynter, 1982], AMNH 69674–69678.

113. **Latal** [= Quebrada Latal; = Quebrada Los Mangos; = Quebrada Panela], 3100 ft [945 m; 10°10′N, 63°57′W; G.H.H. Tate field notes, 1925; DCN, 1964c, unknown year a; not Paynter, 1982], AMNH 69697–69751.

114. **Mount Turumiquire** [= Cerro Turimiquire], 6000 ft [1829 m; 10°07′N, 63°53′W; DCN, 1964c], FMNH 38055.

115. Cumaná, **La Hormiga**, 2000 ft [610 m; not located], BM(NH) 0.5.1.45, 0.5.1.46.

116. **Serranía de Marigüitar**, 450 m [precise location within serranía not available; a locality at 450 m between town of Marigüitar and Cerro Marigüitar would have coordinates of ca. 10°22′N, 63°56′W; DCN, 1970d], MBUCV I-199, 200.

## VARGAS

117. **Camurí Grande**, Núcleo Universidad Simón Bolívar [ca. sea level; 10°37′N, 66°43′W; DCN, 1964a; Aguilera et al., 1995b], MCNUSB I-1011, 1110, 1148.

118. **Macuto** [ca. sea level; 10°36′N, 66°54′W; DCN, 1964a; not Paynter, 1982], USNM 102736.

119. **San Julián** [ca. 120 m; 10°36′N, 66°51′W; DCN, 1964a; but see Paynter, 1982], USNM 143793–143795.

120. **Canales de Naiguatá**, 720–750 m [ca. 10°35′N, 66°44′W; López-Fuster et al., 2000; see also DCN, 1964a; Valdez et al., 1985; not Voss, 1988], MHNLS 8539, 8569, 8574, 8582, 8587, 8590, 8593, 8596, 8599, 8600, 8602, 8603, 8610–8612, 8614, 8615, 8617, 8620, 8623, 8625–8629, 8631–8633, 8636, 8637, 8639, 8641, 8643–8645, 8648–8652, 8654, 8656, 8658, 8660, 8663, 8666–8668, 8673, 8675, 8677, 8679, 8681, 8685, 8686, 8688, 8690, 8694, 8695, 8698, 8699, 8702, 8705, 8706, 8708, 8709, 8715–8717, 8719, 8721, 8726; **Canales de Naiguatá**, vertiente N, Parque Nacional El Ávila, 720 m [same coordinates], MHNLS 8529–8531, 8534; **Los Canales de Naiguatá**, Parque Nacional El Ávila, 800 m [same coordinates], MBUCV I-2713, 2714, 2717; and Parque Nacional El Ávila, Sector Naiguatá [= **Los Canales de Naiguatá**], 720 m [same coordinates], MHNLS 4865, 4868, 4911, 4912, 4915. See also locality 160 for specimens of *H. catopterius* from the same locality.

121. **Carretera El Limón–Puerto La Cruz**, Hacienda El Limón, 300 m [10°32′N, 67°20′W; coordinates correspond to indicated elevation along road between El Limón and Puerto La Cruz; DCN, 1971c], MHNLS 1582; and **Suapo**, Hacienda El Limón, 100 m [same coordinates; coordinates correspond to indicated elevation on

Río Suapo; not Paynter, 1982], MHNLS 2482, 2587.

122. **Cagüita**, Hacienda El Limón, 300 m [10°31′N, 67°19′W; DCN, 1971c; but see Paynter, 1982], MHNLS 1841.
123. **3 km S and 46 km W Caracas**, near El Limón [= Hacienda Carapiche, 48 km W Caracas, Handley, 1976], 398 m [10°29′N, 67°19′W; Handley, 1976], USNM 387819–387821.
124. **La Cochinera**, Hacienda El Limón [small area with swine, W of Río El Limón, between El Limón and Las Llanadas; M. Lentino-R., in litt.], 500 m [10°28′N, 67°19′W; DCN, 1971c; Savini, 1999], MHNLS 2558; and **Las Llanadas**, Hacienda El Limón, 600 m [same coordinates; coordinates correspond to indicated elevation on Quebrada Las Llanadas; but see Paynter, 1982], MHNLS 2736, 2738, 2739.

### UNKNOWN STATE

–. No specific locality, BM(NH) 47.2.1.7 (skull 47.3.26.34; lectotype of *Perognathus bicolor*), 47.2.1.5 (lectoparatype of *Perognathus bicolor*), 47.2.1.4 (skull 47.3.26.35; lectotype of *Heteromys melanoleucus*), 47.2.1.6 (lectoparatype of *Heteromys melanoleucus*).

### *Heteromys catopterius* (total 356)
### VENEZUELA (total 356)

### ARAGUA

125. Monumento Nacional **Pico Codazzi**, Colonia Tovar, 2425 m [10°25′N, 67°19′W; coordinates correspond to indicated elevation; DCN, 1971c], EBRG 22005.
126. Monumento Codazzi, ca. de la **Colonia Tovar**, 1800–2000 m [10°25′N, 67°17′W; DCN, 1971c], EBRG 21410–21422; Monumento Codazzi, **Colonia Tovar**, 1600–2000 m [same coordinates], EBRG 21736; and Monumento Codazzi, entrada **Colonia Tovar**, vía acueducto, 2000 m [same coordinates], EBRG 21408, 21409, 21423–21426, 21432–21434.
127. Monumento Nacional Pico Codazzi, **3 km SW Colonia Tovar** [1700–2100 m; 10°24′N, 67°20′W; DCN, 1971c; Moscarella-T. and Aguilera-M., 1999], MCNUSB I-1363, 1364.
128. Monumento Codazzi, **12.1 km vía Los Gabontes, Colonia Tovar**, 1730 m [10°23′N, 67°20′W; coordinates correspond to indicated elevation along road; DCN, 1971c], EBRG 21429, 21430.
129. **Carretera Estación Biológica Rancho Grande–Cata, km 29**, Parque Nacional Henri Pittier, 680 m [10°22′N, 67°44′W; coordinates correspond to indicated elevation along road; DCN, 1971b], MIZA 20-272, 20-276. See also locality 44 for specimens of *H. anomalus* from the same locality.
130. **Carretera de Ocumare [de la Costa], lado norte**, 920 m [10°22′N, 67°42′W; Beebe and Crane, 1947: 48; DCN, 1971b], MIZA 20-344; **Carretera Estación Biológica Rancho Grande–Cata, km 24**, 900 m [same coordinates], MIZA 20-270; **Carretera Estación Biológica Rancho Grande–Cata, km 24**, Parque Nacional Henri Pittier, 900 m [same coordinates], MIZA 20-275, 20-280, 20-281; **La Regresiva**, Rancho Grande [ca. 900–1000 m; same coordinates; R. Visbal, personal commun.; DCN, 1971b], EBRG 33; **Vía Ocumare de la Costa** [N slope, Schmid et al., 1992], 940 m [same coordinates; but see Schmid et al., 1992], MIZA 20-392, 20-393, 20-394; and **Vía Ocumare de la Costa**, vertiente norte, Parque Nacional Henri Pittier, 940 m [same coordinates; but see Schmid et al., 1992], MIZA 20-391. See also locality 45 for specimens of *H. anomalus* from the same locality.
131. Cerca del pluviometro de Andy Field, abajo de **Pico Guacamaya**, 1690 m [10°22′N, 67°40′W; DCN, 1971b; not Paynter, 1982], MIZA 20-375; Cerca del pluviometro de Andy Field, Parque Nacional Henri Pittier [near **Pico Guacamaya**], 1690 m [same coordinates], MIZA 20-373; Cerca del refugio, **Pico Guacamaya**, Parque Nacional Henri Pittier, 1730 m [same coordinates], MIZA 20-435; El refugio, **Pico Guacamaya**, Parque Nacional Henri Pittier, 1695 m [same coordinates], MIZA 20-376; **La Cumbre**, Estación Biológica Rancho Grande, 1500 m [same coordinates; R. Visbal, personal commun.], MIZA 20-436; Pico Limón [= **Pico Guacamaya**], Rancho Grande, [ca.] 13 km NW Maracay, 4900 ft [1494 m; same coordinates], USNM 517548–517552; and Vía **Pico Guacamaya**, Parque Nacional Henri Pittier, 1810 m [same coordinates], MIZA 20-374.
132. **Headwaters Río Limón**, [ca.] 13 km NW Maracay [ca. 1600 m; 10°22′N, 67°39′W; DCN, 1971b], USNM 517547.
133. Monumento Codazzi, **10 km vía Costa de Maya, Colonia Tovar**, 2110 m [10°22′N, 67°18′W; coordinates correspond to indicated elevation along road; DCN, 1971c], EBRG 21427, 21431.
134. Monumento Codazzi, **16.2 km vía Costa de Maya, Colonia Tovar**, 1840 m [10°22′N, 67°17′W; coordinates correspond to indicated elevation along road; DCN, 1971c], EBRG 21428.
135. **Palo Vaca** [straight stretch of road below La Regresiva, R. Visbal, personal commun.], Rancho Grande [ca. 800–900 m; 10°21′N, 67°42′W; DCN, 1971b], MBUCV I-1235.
136. **El Portachelo**, Rancho Grande, 14 km NW Maracay, 3708 ft [1130 m; 10°21′N, 67°41′W; C.O. Handley, Jr. field notes, 1960; DCN, 1971b; but see Paynter, 1982], USNM 517568; **El Portachuelo**, Parque Nacional Henri Pittier, 1100 m [same coordinates], MIZA 20-472; **El Portachuelo**, Rancho Grande, 14 km NW Maracay, 3708 ft [1130 m; same coordinates], EBRG 363; USNM 517553–517557, 517560–517562; Pico El Periquito, **El Portachuelo**, Rancho Grande [same coordinates], EBRG 191; Pico Periquito, **El Portachuelo**, Rancho Grande [same coordinates], EBRG 362; **Portachuelo**, Parque Nacional Henri Pittier, 1100–1120 m [same coordinates],

MCNUSB I-1326, 1327, 1329–1333; MIZA 20-217, 20-226, 20-234; Rancho Grande, **El Portachuelo** [same coordinates], MBUCV I-1249; and Rancho Grande, **Portachuelo**, 1100 m [same coordinates], MBUCV I-198.

137. **Rancho Grande**, 1080–1100 m [10°21′N, 67°40′W; DCN, 1971b; Handley, 1976; but see Paynter, 1982], AMNH 144848, 144853–144858, 144860, 144864–144868; EBRG 4317; KU 120294, 120295; MBUCV I-295, 1247, 2774, 2775; MCNUSB I-1056, 1057; UMMZ 110768–110773, 110781–110784; USNM 562956; UWZM S.31418; **Rancho Grande Biological Station**, 13 km NW Maracay, 1050 m [same coordinates], USNM 517543; **Rancho Grande**, near **Biological Station**, 13 km NW Maracay, 3576 ft [1090 m; same coordinates], USNM 517533–517535, 517536 (holotype of *Heteromys catopterius*) 517537–517541, 517545, 517546, 517558, 517559, 517563–517567, 517569; **Rancho Grande**, Parque Nacional Henri Pittier [same coordinates], MCNUSB I-1357; alrededores **Estación Biológica Rancho Grande** [same coordinates], EBRG 187, 190; Camino de La Cumbre, **Rancho Grande** [same coordinates], EBRG 189; **Estación Biológica Rancho Grande** [same coordinates], MCNUSB I-423, 424, 581; La toma, Parque Nacional Henri Pittier, **Estación Biológica Rancho Grande**, 1100 m [same coordinates], MIZA 20-173; La toma, **Rancho Grande**, Parque Nacional Henri Pittier, 1100 m [same coordinates], EBRG 10210; MIZA 20-130; Parque Nacional Henri Pittier, camino a la toma, **Rancho Grande**, 1100 m [same coordinates], MIZA 20-028; Parque Nacional Henri Pittier, **Estación Biológica Rancho Grande**, 1100 m [same coordinates], MIZA 20-024, 20-063; Parque Nacional Henri Pittier, **Estación Biológica Rancho Grande**, camino a la toma, 1100 m [same coordinates], MIZA 20-049; Parque Nacional Henri Pittier, más arriba de la **Estación Biológica [de Rancho Grande**], 1300 m [same coordinates], MBUCV I-1795; Pico de Las Vegas, **Rancho Grande** [same coordinates], MBUCV I-1243–1246; Pico La Toma, **Rancho Grande** [same coordinates], EBRG 32; Toma de agua, **Rancho Grande**, Parque Nacional Henri Pittier, 1100 m [same coordinates], EBRG 4319; vicinity Maracay, **Rancho Grande** [same coordinates], UF 13709, 13710; and **Rancho Grande**, 13 km NW Maracay, 1080–1100 m [same coordinates], USNM 371016 (provisional identification only for USNM 371016; see Sympatry and Zones of Contact with *Heteromys anomalus*). See also locality 47 for specimens of *H. anomalus* from the same locality.

138. **Campamento Rafael Rangel** [Sierra Maestra, Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.], 1260 m [10°09′N, 67°09′W; DCN, 1972a; not Voss, 1992; or Adams and Lewis, 1995], USNM 317700, 317702, 317704, 317708, 317711, 317712; **Campamento Rangel** [Sierra Maestra; Brennan, 1952, 1957; = **Minas de Niquel**, R. Guerrero, in litt.; same coordinates], USNM 314815, 314816; and Loma de Hierro [= **Minas de Niquel**, J. Ochoa-G., in litt.], 10 km [by road] WNW [NNE] de Tiara, 1200 m [same coordinates], EBRG 16942. See also locality 53 for specimens of *H. anomalus* from the same locality.

139. **Carretera Choroní, hidrología** [precise location along road from Maracay to Choroní not available], MHNLS 4126.

140. **Parque Nacional Henri Pittier, carretera hacia Ocumare [de la Costa]**, 850 m [precise location along road not available; the indicated elevation on N slope near other known localities of *H. catopterius* would have coordinates of 10°21′N, 67°43′W; DCN, 1971b], MBUCV I-1791–1794.

## CARABOBO

141. **Campamento La Justa**, Rio Morón, 350 m [10° 23′N, 68°14′W; DCN, 1983; Bisbal-E., 1993], EBRG 17109, 17170, 17296.

142. **Parque Nacional San Esteban**, Cariaprima [1025 m; P.J. Soriano, in litt.; 10°22′N, 68°02′W; coordinates correspond to indicated elevation along Río Goaigoaza above Cariaprima; DCN, 1983], EBRG 22006.

143. **Campamento Palmichal**, Pica San Marcos, 780 m [10°20′N, 68°13′W; DCN, 1976c, 1983; Bisbal-E., 1993], EBRG 17189, 17297.

144. **Campamento Palmichal**, 1000 m [10°18′N, 68° 14′W; DCN, 1976c; Bisbal-E., 1993], EBRG 17135; and **Palmichal**, 23 km [by road] N Bejuma, 1000 m [same coordinates; not Musser et al., 1998], MIZA 20-064; USNM 562957.

## DISTRITO CAPITAL

145. **5 km S and 23 km W Caracas, Alto Ño León** [= 31 km WSW Caracas; 1870–1880 m; USNM archives; on S slope along Caracas–Tovar road, ca. 2.5 km W of junction with road to Caracaya; 10°26′N, 67°09′W; N.E. Peterson field notes, 1965, 1967; USNM archives; DCN, 1971c; but see Handley, 1976], EBRG 15082–15084.

## DISTRITO CAPITAL/MIRANDA

146. 1 km N Caracas, **Quebrada Chacaito**, 1170 m [10°32′N, 66°52′W; coordinates correspond to indicated elevation; DCN, 1964a; not Handley, 1976], USNM 405984, 405985; and **Quebrada Chacaito**, Parque Nacional El Ávila, 1200 m [same coordinates; coordinates correspond to indicated elevation], MHNLS 10064, 10068.

147. **Quebrada Chacaito**, 1050 m [10°31′N, 66°52′W; coordinates correspond to indicated elevation; DCN, 1964a; but see Handley, 1976], MHNLS 10599.

## DISTRITO CAPITAL/MIRANDA/VARGAS

148. **Fila El Ávila, Parque Nacional El Ávila**, 1925 m [precise location in park along Fila El Ávila not available], EBRG 20892.

### DISTRITO CAPITAL/VARGAS

149. **Boca de Tigre**, Fila El Ávila, Parque Nacional El Ávila, 1900 m [10°33′N, 66°54′W; DCN, 1964a, 1976a], MHNLS 10491–10493.
150. **El Junquito**, 1900 m [10°28′N, 67°05′W; Paynter, 1982; DCN, 1971c], MBUCV I-293.

### MIRANDA (see also other localities shared with DISTRITO CAPITAL)

151. **Hacienda Las Planadas** [= ca. 25 km (by road) N of Guatire; 1270 m; Rivas and Salcedo, 2006; 10°32′N, 66°30′W; coordinates correspond to indicated elevation; DCN, 1964a; DCN, 1979a], MCNUSB I-1570, 1571.
152. **19 km E Caracas, Curupao** [= 5 km NNW Guarenas, Handley, 1976], 1160–1260 m [10°31′N, 66°38′W; coordinates correspond to indicated elevation above Curupao; Handley, 1976; not Voss, 1991], EBRG 15079; USNM 387829–387831.
153. **Curupao** [ca. 500 m; 10°30′N, 66°38′W; DCN, 1964a; note that Curupao lies at the base of the Cordillera de la Costa in an area that is highly heterogeneous topographically and environmentally; precise collection locality (and corresponding elevation) not available], CUVC 11112.
154. **5 km S and 25 km W Caracas, Alto Ño León** [= 33 km WSW Caracas; 1958–1981 m; USNM archives; 10°26′N, 67°10′W; although other areas were sampled concurrently, these specimens derive from S slope, along Caracas–Tovar road, ca. 4.5 km W of junction with road to Caracaya; C.O. Handley, Jr., in litt.; N.E. Peterson field notes, 1967; USNM archives; DCN, 1971c; but see Handley, 1976], USNM 409802–409805, 409809; and **Alto Ño León, 33 km WSW Caracas** [1967 m, USNM archives; same coordinates], USNM 495293.
155. **Estación Experimental Jaime Hinao J.**, Facultad de Agronomía UCV [Universidad Central de Venezuela], El Laurel, carretera Hoya de la Puerta, 1355 m [10°23′N, 66°54′W; coordinates correspond to indicated elevation along road between Hoya de la Puerta and Cortada del Guayabo; DCN, 1995], EBRG 22259.

### MIRANDA/VARGAS

156. 9.4 km N Caracas, **Hotel Humboldt** [= 5 km NNE Caracas, Handley, 1976], 1982–2223 m [10°33′N, 66°52′W; although other areas were sampled concurrently, these specimens derive from an area NE of Hotel Humboldt, apparently near crest of El Ávila range possibly entirely within Estado Vargas, M.D. Tuttle field notes, 1965; DCN, 1964a; Handley, 1976], EBRG 15052–15056, 15059–15061, 15064, 15065, 15067–15070, 15073, 15074; USNM 370977, 370979–370981, 370983, 370984, 370987, 370988, 370990–370993, 370997–371000, 371003–371006, 371008, 371009, 371011–371013, 372492, 372494, 372495, 374689, 374690; 9.4 km [N] Caracas, **Hotel Humboldt** [= 5 km NNE Caracas, Handley, 1976], 2124 m [same coordinates], EBRG 15071, 15072; Pico Ávila, 5 km NNE Caracas, cerca **Hotel Humboldt**, 2124 m [same coordinates], EBRG 16681; Pico Ávila, 5 km NNE Caracas, near **Hotel Humboldt**, 2103–2221 m [same coordinates], USNM 495286–495288; and **Boquerón**, Parque Nacional El Ávila, 1970 m [same coordinates; DCN, 1964a, 1976a; see also SAGCN, 1994], MHNLS 10613.

### MONAGAS

157. **San Agustín**, 5 km NW Caripe, 1270 m [10°12′N, 63°32′W; DCN, 1964c; Handley, 1976], USNM 495295.
158. **3 km N and 2 km W Caripe, Hacienda San Fernando** [= 3 km NW Caripe, Handley, 1976], 1320 m [10°12′N, 63°31′W; N.E. Peterson field notes, 1967; DCN, 1964c; but see Handley, 1976], USNM 409818.
159. **2 km N and 4 km W Caripe, La Laguna** [= 5 km NW Caripe, Handley, 1976], 1170–1335 m [10°11′N, 63°32′W; N.E. Peterson field notes, 1967; DCN, 1964c; but see Handley, 1976], EBRG 15088; USNM 409817, 409823; and **2 km N and 4 km W Caripe**, near San Agustín [= 5 km NW Caripe, Handley, 1976], 1170–1180 m [same coordinates], EBRG 15086, 15087. See also locality 84 for specimens of *H. anomalus* from the same locality.

### VARGAS (see also other localities shared with DISTRITO CAPITAL and MIRANDA)

160. **Canales de Naiguatá**, vertiente N, Parque Nacional El Ávila, 720 m [ca. 10°35′N, 66°44′W; López-Fuster et al., 2000; see also DCN, 1964a; Valdez et al., 1985; not Voss, 1988], MHNLS 8532, 8533, 8535–8538; **Canales de Naiguatá**, 720 m [same coordinates], MHNLS 8576, 8583, 8585, 8586, 8588, 8589, 8591, 8592, 8595, 8597, 8601, 8605, 8606, 8616, 8618, 8621, 8622, 8624, 8634, 8638, 8642, 8647, 8653, 8655, 8657, 8661, 8662, 8669, 8670, 8672, 8676, 8678, 8680, 8683, 8684, 8687, 8689, 8691–8693, 8696, 8700, 8703, 8704, 8707, 8710–8714, 8720, 8722, 8725; **Canales de Naiguatá**, Parque Nacional El Ávila, 720–800 m [same coordinates], MBUCV I-2720–2724, 2726; MHNLS 8604, 8723; **Los Canales de Naiguatá**, 720 m [same coordinates], CUVC 11113; **Los Canales de Naiguatá**, Parque Nacional El Ávila, 800 m [same coordinates], MBUCV I-2715, 2716, 2718; Parque Nacional El Ávila, **Los Canales de Naiguatá**, 800 m [same coordinates], UV 11830 (= MBUCV I-2719), 11831 (= MBUCV I-2725); Parque Nacional El Ávila, Sector Naiguatá [= **Los Canales de Naiguatá**],

720 m [same coordinates], MHNLS 4866, 4867, 4913, 4914, 4916, 4917; Río Camurí Grande, **Los Canales de Naiguatá**, 15.6 km ramal este [same coordinates], MCNUSB I-1358; and **[Los Canales de] Naiguatá**, 720 m [same coordinates], MHNLS 4918. See also locality 120 for specimens of *H. anomalus* from the same locality.

161. **El Aguacatal**, Hacienda El Limón, 1400 m [10° 27′N, 67°16′W; DCN, 1971c], MHNLS 2684.
162. **Las Aguaitas**, Hacienda El Limón, 2000 m [10° 26′N, 67°18′W; coordinates correspond to indicated elevation on Río El Limoncito N of Colonia Tovar; DCN, 1971c; see also Paynter, 1982], MHNLS 2079, 3431; and **Las Aguaitas**, N Colonia Tovar, 2000 m [same coordinates], MHNLS 2441, 2614, 2615.

## APPENDIX 2

### Other Specimens Examined (Outside Principal Study Area)

See Gazetteer (appendix 1) for specimens examined from the principal study area.

***Heteromys anomalus*** **(total 56): COLOMBIA (13): Cundinamarca**: Caparrapí, Volcanes, ICN 409, 1827–1831, 1832 (holotype of *Heteromys anomalus hershkovitzi*), 1833–1835, 1866; **Magdalena**: below Minca, 1000 feet [305 m], AMNH 15347 (holotype of *Heteromys jesupi*), 15348. **VENEZUELA (43): Barinas**: El Cobalongo, 7 km NNE Altamira [900 m, Handley, 1976; 8°53′N, 70°28′W; A.L. Tuttle field notes, 1967; DCN, 1975a; not Handley, 1976], USNM 416691; **Falcón**: El Mene [not located; multiple towns and geographic features named Mene are present in Estado Falcón], BM(NH) 26.12.6.1.; **Lara**: El Blanquito, 9 km [airline] SE de Sanare, Parque Nacional Yacambú, 1650 m, CVULA I-2728, 2732, 2736, 2742, 2743, 2750, 2754, 2755; El Blanquito, 17 km [by road] SE de Sanare, Parque Nacional Yacambú, 1600 m, CVULA I-6162; MCNUSB I-808, 809, 812, 813, 816, 852–855; El Blanquito, 17–18 km [SE by road] de Sanare, Parque Nacional Yacambú, 1500 m, EBRG 10302; Parque Nacional Yacambú [near El Blanquito; J. Ochoa-G., in litt.], 1500–1650 m, MBUCV I-4844, 4848, 4867; **Trujillo**: 10 km WNW Valera, Isnotú, 930 m, USNM 371034; **Zulia**: El Tucuco [= Los Ángeles del Tucuco], 46 km SSW Machiques, 300–400 m, CVULA I-1890; Misión Tukuko, 200–400 m, MHNLS 7711, 7781, 7803, 7806, 7808; USNM 448546, 448547, 448556, 448558, 448559, 448561; Río Aurare, FMNH 18622, 18623 (holotype of *Heteromys anomalus brachialis*), 18624–18627. See Anderson (2003b) for additional specimens from Colombia and western Venezuela.

***Heteromys australis*** **(total 26): COLOMBIA (1): Valle del Cauca**: Las Lomitas, 5000 ft [1524 m], AMNH 32240 (holotype of *Heteromys lomitensis*). **ECUADOR (10): Esmeraldas**: San Javier [= San Javier de Cachaví], 60–120 ft [18–37 m], BM(NH) 1.3.19.19, 1.3.19.20, 1.3.19.21, 1.3.19.22, 1.3.19.23 (holotype of *Heteromys australis*), 1.3.19.24; USNM 113304–113307. **PANAMÁ (15): Darién**: Cana, 1800–2000 ft [549–610 m], USNM 178621, 178698, 178699 (holotype of *Heteromys australis consicus*), 178700, 179595; Amagal, 1000–2000 ft [305–610 m], ANSP 19491–19498, 19499 (holotype of *Heteromys australis pacificus*), 19779. See Anderson (1999) for additional specimens from Colombia, Panama, and western Venezuela; and Anderson and Jarrín-V. (2002) for additional specimens from Ecuador.

***Heteromys desmarestianus*** **(species complex; total 87): COSTA RICA (11): Cartago**: Angostura, USNM 12903/38590, 12904/38591 (holotype of *Heteromys desmarestianus subaffinis*), 12905/36848; **San José**: Escazú, 3000 ft [914 m], AMNH 131729 (holotype of *Heteromys desmarestianus underwoodi*); Escazú, Los Higuerones, AMNH 137299–137302; San Gerónimo Pirris, USNM 250348 (holotype of *Heteromys desmarestianus planifrons*), 250349, 256445. **EL SALVADOR: (8): Chalatenango:** Los Esesmiles, 8000 ft [2439 m], MVZ 131116, 131117, 131119, 131121–131124, 131126 (paratypes of *Heteromys desmarestianus psakastus*). **GUATEMALA (1): Alta Verapaz:** Cobán, BM(NH) 43.6.13.1 (holotype of *Heteromys desmarestianus*). **MÉXICO (23): Chiapas**: Chicharras, USNM 77576 (holotype of *Heteromys goldmani*), 77577, 77579–77582, 77694; Mountains near Tonala, USNM 76062 (holotype of *Heteromys griseus*), 76063–76070; **Oaxaca**: Mountains near Santo Domingo, USNM 73381, 73382 (holotype of *Heteromys goldmani lepturus*); Tehuantepec, Mazatlán, AMNH 165995 (holotype of *Heteromys nigricaudatus*); **Veracruz**: Motzorongo, USNM 63718, 63719 (holotype of *Heteromys temporalis*), 63720; **Unknown State**: no specific locality, BM(NH) 56.8.1.13 (holotype of *Heteromys longicaudatus*). **NICARAGUA (1)**: **Matagalpa**: Tuma, AMNH 28451 (holotype of *Heteromys fuscatus*). **PANAMÁ (43): Colón**: Río Indio, near Gatún, USNM 170919, 170920, 170975, 170976 (holotype of *Heteromys zonalis*); **Chiriquí**: Boquete, 4000–5800 ft [1219–1768 m], MCZ B10355, B10356 (holotype of *Heteromys repens*), B10358, B10360, B10361; Cerro Pando, ANSP 17835 (holotype of *Heteromys desmarestianus chiriquensis*), 17836, 17837, 18374–18377; **Darién**: Mount Pirri [= Cerro Pirre], near head of Río Limón, 4500–5200 ft [1372–1585 m], USNM 178998–179004, 179006–179015, 179016 (holotype of *Heteromys crassirostris*), 179018–179020; **Panamá**: Cerro Azul, 2500–3000 ft [762–914 m], USNM 171107 (holotype of *Heteromys panamensis*), 171108–171111, 171128. See Anderson (1999) for additional specimens from Colombia and Panama; and Anderson and Timm (2006) for additional specimens from Costa Rica.

***Heteromys gaumeri*** **(total 7): MÉXICO (7): Yucatán**: Chichenitza [= Chichén Itzá], AMNH 12025/10458, 12027/10460, 12028/10461 (holotype of *Heteromys gaumeri*), 12029/10462, 12030/10463, 12031/10464; BM(NH) 97.4.5.3.

***Heteromys nelsoni*** **(total 2): MÉXICO (2): CHIAPAS**: Pinabete, USNM 77920 (holotype of *Heteromys nelsoni*), 77578.

***Heteromys nubicolens*** **(total 9): COSTA RICA (9): PUNTARENAS:** Monteverde, Monteverde Cloud Forest Reserve, Investigator's Trail, 1550 m. KU 159022–159024, 159025 (holotype of *Heteromys nubicolens*) 159026–159029; MNCR 1336; See Anderson and Timm (2006) for additional specimens from Costa Rica.

***Heteromys oasicus*** **(total 7): VENEZUELA (7): FALCÓN**: 49 km N, 32 km W of Coro, Cerro Santa Ana [= 15 km SSW Pueblo Nuevo], 550–615 m, EBRG 15110, 15111; USNM 456325 (holotype of *Heteromys oasicus*), 456327, 495338; Cerro Santa Ana, Península de Paraguaná, 420–550 m, EBRG 3705, 15984. See Anderson (2003b) for additional specimens from Venezuela.

***Heteromys oresterus*** **(total 10): COSTA RICA (10): SAN JOSÉ**: El Copey de Dota, 6000–6500 ft [1829–1981 m], UMMZ 64026, 64027 (holotype of *Heteromys oresterus*), 64028–64034, 66478. See Anderson and Timm (2006) for additional specimens from Costa Rica.

***Heteromys teleus*** **(total 17): ECUADOR (17): GUAYAS**: Cerro Manglar Alto, western slope, AMNH 64680–64693, 64694 (holotype of *Heteromys teleus*), 64695, 64696. See Anderson and Jarrín-V. (2002) for additional specimens from Ecuador.

## APPENDIX 3

### DESCRIPTIVE STATISTICS FOR PRIMARY GEOGRAPHIC SAMPLES

Sample size, mean ± standard error, and range (minimum–maximum) for external variables, mass, cranial measurements, and one derived ratio for adult specimens in age class 4 from primary geographic samples of *Heteromys catopterius* (Rancho Grande and Humboldt) and *H. anomalus* (all other samples; see Materials and Methods and appendices 1 and 2 for provenience). Linear measurements are in millimeters, mass is in grams, and the ratio is multiplied by 100 to yield a percentage.

| | Sample size | Mean ± standard error | Minimum–maximum |
|---|---|---|---|
| *Total length* | | | |
| Rancho Grande | 25 | 302 ± 3 | 270–324 |
| Humboldt | 12 | 288 ± 2 | 275–300 |
| Tukuko | 10 | 280 ± 5 | 257–303 |
| Yacambú | 22 | 292 ± 3 | 262–323 |
| Naiguatá | 1 | 286 ± - | 286 |
| Neverí | 10 | 292 ± 5 | 274–327 |
| Latal | 11 | 293 ± 3 | 279–312 |
| Manacal | 10 | 282 ± 5 | 258–302 |
| *Head-and-body length* | | | |
| Rancho Grande | 26 | 134 ± 2 | 113–149 |
| Humboldt | 12 | 126 ± 2 | 118–138 |
| Tukuko | 10 | 128 ± 2 | 118–140 |
| Yacambú | 22 | 131 ± 2 | 115–151 |
| Naiguatá | 1 | 134 ± - | 134 |
| Neverí | 11 | 128 ± 3 | 117–147 |
| Latal | 11 | 130 ± 2 | 122–143 |
| Manacal | 10 | 126 ± 2 | 117–137 |
| *Tail length* | | | |
| Rancho Grande | 23 | 168 ± 3 | 147–192 |
| Humboldt | 12 | 163 ± 1 | 155–170 |
| Tukuko | 10 | 152 ± 3 | 136–172 |
| Yacambú | 22 | 162 ± 2 | 140–180 |
| Naiguatá | 1 | 152 ± - | 152 |
| Neverí | 10 | 164 ± 2 | 155–180 |
| Latal | 11 | 163 ± 2 | 153–173 |
| Manacal | 10 | 156 ± 4 | 134–175 |
| *Tail length/head-and-body length, × 100 (%)* | | | |
| Rancho Grande | 23 | 126 ± 3 | 100–152 |
| Humboldt | 12 | 130 ± 2 | 112–141 |
| Tukuko | 10 | 119 ± 3 | 108–131 |
| Yacambú | 22 | 124 ± 2 | 109–140 |
| Naiguatá | 1 | 113 ± - | 113 |
| Neverí | 10 | 127 ± 2 | 120–135 |
| Latal | 11 | 125 ± 2 | 113–137 |
| Manacal | 10 | 124 ± 3 | 108–146 |
| *Hind foot length* | | | |
| Rancho Grande | 26 | 36 ± 0 | 33–39 |
| Humboldt | 11 | 34 ± 0 | 32–36 |
| Tukuko | 10 | 35 ± 1 | 33–37 |
| Yacambú | 22 | 34 ± 0 | 32–37 |
| Naiguatá | 1 | 31 ± - | 31 |
| Neverí | 11 | 35 ± 0 | 33–37 |
| Latal | 11 | 36 ± 0 | 34–37 |
| Manacal | 10 | 35 ± 1 | 33–38 |

APPENDIX 3
*(Continued)*

| | Sample size | Mean ± standard error | Minimum–maximum |
|---|---|---|---|
| *Ear length* | | | |
| Rancho Grande | 25 | 20 ± 0 | 16–22 |
| Humboldt | 12 | 17 ± 0 | 14–19 |
| Tukuko | 10 | 17 ± 0 | 15–18 |
| Yacambú | 21 | 19 ± 0 | 17–22 |
| Naiguatá | 0 | – | – |
| Neverí | 0 | – | – |
| Latal | 0 | – | – |
| Manacal | 10 | 19 ± 0 | 17–20 |
| *Mass* | | | |
| Rancho Grande | 19 | 82 ± 4 | 59–119 |
| Humboldt | 0 | – | – |
| Tukuko | 10 | 72 ± 4 | 58–100 |
| Yacambú | 20 | 57 ± 2 | 42–74 |
| Naiguatá | 0 | – | – |
| Neverí | 0 | – | – |
| Latal | 0 | – | – |
| Manacal | 10 | 60 ± 4 | 49–87 |
| *Occipitonasal length* | | | |
| Rancho Grande | 32 | 36.98 ± 0.15 | 35.13–38.66 |
| Humboldt | 14 | 35.87 ± 0.14 | 34.74–36.71 |
| Tukuko | 12 | 35.59 ± 0.50 | 31.94–39.02 |
| Yacambú | 22 | 34.65 ± 0.22 | 32.13–35.90 |
| Naiguatá | 17 | 34.84 ± 0.43 | 31.06–38.36 |
| Neverí | 11 | 36.35 ± 0.36 | 34.89–38.85 |
| Latal | 11 | 36.53 ± 0.25 | 35.15–37.90 |
| Manacal | 10 | 35.19 ± 0.46 | 32.85–38.04 |
| *Zygomatic breadth* | | | |
| Rancho Grande | 32 | 17.06 ± 0.09 | 16.07–18.17 |
| Humboldt | 14 | 16.05 ± 0.09 | 15.52–16.57 |
| Tukuko | 12 | 16.55 ± 0.23 | 15.12–17.90 |
| Yacambú | 22 | 16.20 ± 0.11 | 15.04–16.87 |
| Naiguatá | 17 | 15.76 ± 0.16 | 14.42–16.80 |
| Neverí | 11 | 16.68 ± 0.17 | 15.93–17.61 |
| Latal | 11 | 16.22 ± 0.15 | 15.46–16.89 |
| Manacal | 10 | 16.02 ± 0.18 | 14.90–16.95 |
| *Rostral length* | | | |
| Rancho Grande | 32 | 16.41 ± 0.09 | 15.26–17.57 |
| Humboldt | 14 | 16.01 ± 0.14 | 14.98–16.86 |
| Tukuko | 12 | 15.51 ± 0.23 | 13.94–17.01 |
| Yacambú | 22 | 15.41 ± 0.12 | 13.69–16.20 |
| Naiguatá | 17 | 15.41 ± 0.19 | 13.60–16.63 |
| Neverí | 11 | 16.29 ± 0.21 | 15.39–17.60 |
| Latal | 11 | 16.32 ± 0.16 | 15.38–16.97 |
| Manacal | 10 | 15.38 ± 0.24 | 14.48–17.00 |
| *Nasal length* | | | |
| Rancho Grande | 32 | 14.90 ± 0.09 | 13.70–15.93 |
| Humboldt | 14 | 14.21 ± 0.16 | 13.45–15.33 |
| Tukuko | 12 | 14.29 ± 0.24 | 12.74–16.10 |
| Yacambú | 22 | 14.10 ± 0.12 | 12.74–15.47 |

APPENDIX 3
*(Continued)*

| | Sample size | Mean ± standard error | Minimum–maximum |
|---|---|---|---|
| Naiguatá | 17 | 13.96 ± 0.22 | 11.93–15.35 |
| Neverí | 11 | 14.60 ± 0.22 | 13.79–16.04 |
| Latal | 11 | 14.81 ± 0.14 | 14.11–15.51 |
| Manacal | 10 | 14.00 ± 0.23 | 12.65–15.32 |
| *Least interorbital constriction* | | | |
| Rancho Grande | 32 | 9.29 ± 0.07 | 8.59–10.13 |
| Humboldt | 14 | 8.76 ± 0.07 | 8.13–9.05 |
| Tukuko | 12 | 8.68 ± 0.14 | 8.10–9.78 |
| Yacambú | 22 | 8.37 ± 0.05 | 7.99–8.78 |
| Naiguatá | 17 | 8.31 ± 0.08 | 7.81–8.87 |
| Neverí | 11 | 8.38 ± 0.11 | 7.89–9.00 |
| Latal | 11 | 8.53 ± 0.08 | 8.18–9.07 |
| Manacal | 10 | 8.00 ± 0.10 | 7.66–8.60 |
| *Squamosal breadth* | | | |
| Rancho Grande | 32 | 15.64 ± 0.07 | 15.02–16.56 |
| Humboldt | 14 | 15.09 ± 0.07 | 14.67–15.52 |
| Tukuko | 12 | 15.26 ± 0.14 | 14.13–16.00 |
| Yacambú | 22 | 14.85 ± 0.09 | 14.24–15.81 |
| Naiguatá | 17 | 15.02 ± 0.11 | 14.09–15.69 |
| Neverí | 11 | 15.08 ± 0.10 | 14.65–15.74 |
| Latal | 11 | 15.16 ± 0.09 | 14.46–15.50 |
| Manacal | 10 | 14.78 ± 0.13 | 14.21–15.45 |
| *Maxillary toothrow length* | | | |
| Rancho Grande | 32 | 5.60 ± 0.04 | 5.17–5.94 |
| Humboldt | 14 | 5.48 ± 0.05 | 5.14–5.70 |
| Tukuko | 12 | 5.42 ± 0.07 | 4.87–5.80 |
| Yacambú | 22 | 5.49 ± 0.05 | 5.04–6.05 |
| Naiguatá | 17 | 5.13 ± 0.05 | 4.67–5.45 |
| Neverí | 11 | 5.52 ± 0.06 | 5.26–5.83 |
| Latal | 11 | 5.47 ± 0.05 | 5.17–5.76 |
| Manacal | 10 | 5.21 ± 0.09 | 4.80–5.67 |
| *Interparietal width* | | | |
| Rancho Grande | 32 | 9.83 ± 0.09 | 8.57–11.01 |
| Humboldt | 14 | 8.49 ± 0.12 | 7.72–9.52 |
| Tukuko | 12 | 9.60 ± 0.13 | 8.85–10.30 |
| Yacambú | 22 | 8.59 ± 0.12 | 7.56–9.79 |
| Naiguatá | 17 | 8.67 ± 0.17 | 7.06–9.93 |
| Neverí | 11 | 8.71 ± 0.12 | 8.02–9.11 |
| Latal | 11 | 8.45 ± 0.10 | 7.94–8.97 |
| Manacal | 10 | 8.50 ± 0.14 | 7.70–9.33 |
| *Interparietal length* | | | |
| Rancho Grande | 32 | 5.04 ± 0.08 | 3.95–6.07 |
| Humboldt | 14 | 4.68 ± 0.09 | 3.95–5.17 |
| Tukuko | 12 | 5.22 ± 0.10 | 4.64–5.67 |
| Yacambú | 22 | 4.77 ± 0.08 | 4.03–5.51 |
| Naiguatá | 17 | 4.86 ± 0.11 | 4.09–5.63 |
| Neverí | 11 | 5.38 ± 0.06 | 5.13–5.83 |
| Latal | 11 | 5.11 ± 0.06 | 4.86–5.39 |
| Manacal | 10 | 5.27 ± 0.14 | 4.37–5.73 |

APPENDIX 3
*(Continued)*

| | Sample size | Mean ± standard error | Minimum–maximum |
|---|---|---|---|
| *Parietal breadth* | | | |
| Rancho Grande | 32 | 13.28 ± 0.07 | 12.61–14.00 |
| Humboldt | 14 | 12.68 ± 0.07 | 11.91–13.01 |
| Tukuko | 12 | 12.85 ± 0.15 | 12.29–13.94 |
| Yacambú | 22 | 12.53 ± 0.08 | 11.72–13.29 |
| Naiguatá | 17 | 12.34 ± 0.08 | 11.67–13.15 |
| Neverí | 11 | 12.61 ± 0.10 | 12.10–13.11 |
| Latal | 11 | 12.73 ± 0.10 | 11.97–13.05 |
| Manacal | 10 | 12.24 ± 0.06 | 11.97–12.47 |
| *Skull depth* | | | |
| Rancho Grande | 32 | 11.59 ± 0.04 | 11.09–12.07 |
| Humboldt | 14 | 11.03 ± 0.04 | 10.70–11.23 |
| Tukuko | 12 | 11.08 ± 0.10 | 10.35–11.65 |
| Yacambú | 22 | 10.99 ± 0.06 | 10.50–11.57 |
| Naiguatá | 17 | 11.01 ± 0.07 | 10.45–11.62 |
| Neverí | 11 | 11.16 ± 0.06 | 10.79–11.42 |
| Latal | 11 | 11.14 ± 0.08 | 10.52–11.48 |
| Manacal | 10 | 10.72 ± 0.10 | 10.36–11.40 |

## APPENDIX 4

### DESCRIPTIVE STATISTICS FOR LOS CANALES DE NAIGUATÁ

Sample size, mean ± standard error, and range (minimum–maximum) of cranial measurements (in millimeters) for specimens in age classes 1–4 of *Heteromys anomalus* and *H. catopterius* from Los Canales de Naiguatá (localities 120 and 160; see appendix 1 for provenience).

| | Sample size | Mean ± standard error | Minimum–maximum |
|---|---|---|---|
| *H. anomalus*, age class 1 | | | |
| Occipitonasal length | 9 | 28.33 ± 0.51 | 25.03–30.06 |
| Zygomatic breadth | 9 | 13.69 ± 0.19 | 12.54–14.41 |
| Rostral length | 9 | 11.73 ± 0.25 | 9.99–12.57 |
| Nasal length | 9 | 10.49 ± 0.25 | 8.87–11.42 |
| Least interorbital constriction | 9 | 7.35 ± 0.10 | 6.65–7.58 |
| Squamosal breadth | 9 | 13.33 ± 0.15 | 12.32–13.86 |
| Maxillary toothrow length | 9 | 4.72 ± 0.11 | 4.13–5.05 |
| Interparietal width | 9 | 8.24 ± 0.16 | 7.52–8.86 |
| Interparietal length | 9 | 4.58 ± 0.10 | 4.18–5.06 |
| Parietal breadth | 9 | 11.70 ± 0.09 | 11.02–11.92 |
| Skull depth | 9 | 9.97 ± 0.10 | 9.33–10.32 |
| *H. catopterius*, age class 1 | | | |
| Occipitonasal length | 9 | 31.15 ± 0.32 | 29.32–32.59 |
| Zygomatic breadth | 9 | 14.87 ± 0.09 | 14.42–15.30 |
| Rostral length | 9 | 13.16 ± 0.13 | 12.43–13.59 |
| Nasal length | 9 | 11.41 ± 0.19 | 10.56–12.10 |
| Least interorbital constriction | 9 | 8.08 ± 0.09 | 7.68–8.45 |
| Squamosal breadth | 9 | 14.02 ± 0.08 | 13.61–14.38 |
| Maxillary toothrow length | 9 | 5.00 ± 0.10 | 4.40–5.34 |
| Interparietal width | 9 | 8.19 ± 0.08 | 7.79–8.42 |
| Interparietal length | 9 | 4.58 ± 0.10 | 4.28–5.07 |
| Parietal breadth | 9 | 12.50 ± 0.11 | 12.02–13.03 |
| Skull depth | 9 | 10.50 ± 0.10 | 9.88–10.85 |
| *H. anomalus*, age class 2 | | | |
| Occipitonasal length | 13 | 30.48 ± 0.43 | 28.84–34.81 |
| Zygomatic breadth | 13 | 14.33 ± 0.14 | 13.68–15.45 |
| Rostral length | 13 | 12.97 ± 0.24 | 12.09–15.40 |
| Nasal length | 13 | 11.46 ± 0.23 | 10.57–13.59 |
| Least interorbital constriction | 13 | 7.61 ± 0.11 | 7.08–8.38 |
| Squamosal breadth | 13 | 13.85 ± 0.16 | 13.18–15.11 |
| Maxillary toothrow length | 13 | 5.00 ± 0.05 | 4.75–5.30 |
| Interparietal width | 13 | 8.44 ± 0.15 | 7.82–9.48 |
| Interparietal length | 13 | 4.63 ± 0.19 | 3.17–5.90 |
| Parietal breadth | 13 | 12.15 ± 0.12 | 11.23–13.05 |
| Skull depth | 13 | 10.30 ± 0.08 | 9.76–10.84 |
| *H. catopterius*, age class 2 | | | |
| Occipitonasal length | 31 | 32.76 ± 0.27 | 30.40–36.29 |
| Zygomatic breadth | 31 | 15.35 ± 0.12 | 14.55–16.83 |
| Rostral length | 31 | 13.98 ± 0.14 | 12.48–15.68 |
| Nasal length | 31 | 12.19 ± 0.14 | 10.60–14.26 |
| Least interorbital constriction | 31 | 8.45 ± 0.07 | 7.76–9.47 |
| Squamosal breadth | 31 | 14.48 ± 0.09 | 13.82–15.87 |
| Maxillary toothrow length | 31 | 5.26 ± 0.03 | 4.83–5.57 |
| Interparietal width | 31 | 8.71 ± 0.10 | 7.30–9.45 |
| Interparietal length | 31 | 4.38 ± 0.09 | 3.12–5.26 |
| Parietal breadth | 31 | 12.86 ± 0.05 | 12.29–13.53 |
| Skull depth | 31 | 10.90 ± 0.06 | 10.16–11.64 |

APPENDIX 4
*(Continued)*

| | Sample size | Mean ± standard error | Minimum–maximum |
|---|---|---|---|
| *H. anomalus*, age class 3 | | | |
| Occipitonasal length | 20 | 33.90 ± 0.43 | 31.07–37.21 |
| Zygomatic breadth | 20 | 15.16 ± 0.19 | 13.58–16.60 |
| Rostral length | 20 | 14.80 ± 0.22 | 12.75–16.66 |
| Nasal length | 20 | 13.49 ± 0.20 | 12.04–14.75 |
| Least interorbital constriction | 20 | 8.16 ± 0.10 | 7.35–9.09 |
| Squamosal breadth | 20 | 14.62 ± 0.12 | 13.70–15.84 |
| Maxillary toothrow length | 20 | 5.06 ± 0.07 | 4.51–5.60 |
| Interparietal width | 20 | 8.66 ± 0.10 | 7.57–9.41 |
| Interparietal length | 20 | 4.78 ± 0.08 | 4.14–5.52 |
| Parietal breadth | 20 | 12.25 ± 0.08 | 11.57–12.79 |
| Skull depth | 20 | 10.78 ± 0.07 | 10.22–11.51 |
| *H. catopterius*, age class 3 | | | |
| Occipitonasal length | 5 | 35.22 ± 0.70 | 32.77–36.77 |
| Zygomatic breadth | 5 | 15.74 ± 0.21 | 15.05–16.22 |
| Rostral length | 5 | 15.36 ± 0.25 | 14.46–15.79 |
| Nasal length | 5 | 13.64 ± 0.52 | 12.44–15.52 |
| Least interorbital constriction | 5 | 8.82 ± 0.18 | 8.26–9.28 |
| Squamosal breadth | 5 | 15.02 ± 0.23 | 14.44–15.58 |
| Maxillary toothrow length | 5 | 5.31 ± 0.08 | 5.15–5.59 |
| Interparietal width | 5 | 8.87 ± 0.29 | 8.07–9.75 |
| Interparietal length | 5 | 4.77 ± 0.08 | 4.57–5.05 |
| Parietal breadth | 5 | 13.07 ± 0.16 | 12.61–13.49 |
| Skull depth | 5 | 11.29 ± 0.15 | 10.90–11.66 |
| *H. anomalus*, age class 4 | | | |
| Occipitonasal length | 17 | 34.84 ± 0.43 | 31.06–38.36 |
| Zygomatic breadth | 17 | 15.76 ± 0.16 | 14.42–16.80 |
| Rostral length | 17 | 15.41 ± 0.19 | 13.60–16.63 |
| Nasal length | 17 | 13.96 ± 0.22 | 11.93–15.35 |
| Least interorbital constriction | 17 | 8.31 ± 0.08 | 7.81–8.87 |
| Squamosal breadth | 17 | 15.02 ± 0.11 | 14.09–15.69 |
| Maxillary toothrow length | 17 | 5.13 ± 0.05 | 4.67–5.45 |
| Interparietal width | 17 | 8.67 ± 0.17 | 7.06–9.93 |
| Interparietal length | 17 | 4.86 ± 0.11 | 4.09–5.63 |
| Parietal breadth | 17 | 12.34 ± 0.08 | 11.67–13.15 |
| Skull depth | 17 | 11.01 ± 0.07 | 10.45–11.62 |
| *H. catopterius*, age class 4 | | | |
| Occipitonasal length | 5 | 37.77 ± 0.67 | 35.83–39.87 |
| Zygomatic breadth | 5 | 16.79 ± 0.18 | 16.25–17.37 |
| Rostral length | 5 | 16.76 ± 0.28 | 15.79–17.52 |
| Nasal length | 5 | 14.87 ± 0.32 | 13.94–15.58 |
| Least interorbital constriction | 5 | 9.00 ± 0.17 | 8.40–9.38 |
| Squamosal breadth | 5 | 15.23 ± 0.12 | 14.90–15.57 |
| Maxillary toothrow length | 5 | 5.43 ± 0.09 | 5.20–5.69 |
| Interparietal width | 5 | 9.21 ± 0.23 | 8.50–9.65 |
| Interparietal length | 5 | 4.80 ± 0.23 | 4.15–5.44 |
| Parietal breadth | 5 | 12.90 ± 0.15 | 12.60–13.37 |
| Skull depth | 5 | 11.65 ± 0.10 | 11.40–11.95 |