Cryptotis merriami Choate in Costa Rica: Syntopy with *Cryptotis nigrescens* (Allen) and Possible Character Displacement (Mammalia: Insectivora)

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ABSTRACT.—A recent review of small-eared shrews, genus *Cryptotis* (Mammalia: Insectivora: Soricidae), in the collection of the Museo Nacional de Costa Rica, revealed a previously unidentified specimen of *Cryptotis merriami* Choate from the Monteverde Cloud Forest Reserve. This specimen is only the second record of *C. merriami* from Costa Rica, it represents the southernmost record for the species, and it documents the first case of syntopy between *C. merriami* and *Cryptotis nigrescens* (Allen). The co-occurence of *C. merriami* and *C. nigrescens* provides conclusive support for the hypothesis they are distinct species within the *C. nigrescens-*group (*sensu* Woodman and Timm, 1993). The soricid community at Monteverde is comprised of three species in three evenly-spaced size classes: the numerically-dominant *C. nigrescens, C. merriami*, and an undescribed, endemic species the size of typical *C. merriami*. Morphometrical analysis indicated that *C. merriami* exhibits no apparent geographic trends in size throughout most of its range, yet the Monteverde specimen is significantly larger than all other *C. merriami*. Its large size at Monteverde apparently represents character displacement in response to the presence of a more abundant sister species, *C. nigrescens*; the presence of a second, unrelated shrew the size of more typical *C. merriami*; or interactions with both.

INTRODUCTION

Small-eared shrews of the genus *Cryptotis* occur from southernmost Canada and the eastern half of the United States, through Mexico and Central America, to northwestern South America. Choate (1970) partitioned Middle American species into three informal divisions: the *Cryptotis mexicana-*group, the *Cryptotis parva-*group, and a group of "relict species" of unknown, but supposed primitive affinities. The *C. parva-*group included *C. parva* (Say), with six Middle American subspecies, and *Cryptotis nigrescens* (Allen), with three subspecies.

Woodman and Timm (1993, 1999) demonstrated that *C. nigrescens* is a complex of six species (*C. colombiana, C. hondurensis, C. mayensis, C. mera, C. merriami*, and *C. nigrescens*), which they informally called the *Cryptotis nigrescens-*group. Members of the group share a number of morphological characters, some of which may be plesiomorphic within the genus (Woodman and Timm, 1999). These species are small- to

medium-sized (head-and-body length, 53-79 mm; Table 1) small-eared shrews with short- to medium-length tails (usually averaging 39-47% of head-and-body length); unspecialized forefeet; short, narrow foreclaws; simple humeri; broad zygomatic plates; posteriorly-convex unicuspids; and unrecessed upper molariform dentitions. The group is distributed from southern Mexico through Central America to the Eastern Cordillera of Colombia (Woodman and Timm, 1992, 1993; Woodman, 1995, 1996). Although each species is morphologically and morphometrically distinctive, all evidence indicated that species were allopatric, precluding tests of morphological intergradation.

Two species of the *Cryptotis nigrescens-*group occur in Costa Rica. *Cryptotis nigrescens* (*sensu stricto*) occurs at middle to high elevations (800-2900 m) throughout much of Costa Rica and western Panama (Fig. 1). *Cryptotis merriami* Choate has a discontinuous distribution above 900 m from Chiapas, Mexico, to northern Costa Rica, although

TABLE 1. Measurements of *Cryptotis nigrescens* and *Cryptotis merriami* used in this study. Statistics presented are mean ± standard deviation of the mean, and observed extremes. A dash (—) indicates no measurement is available.

Cryptotis nigrescens (Monteverde) $n = 41$ (except as noted)	*Cryptotis merriami*		
	Monteverde	Finca San Bosco	Main geographic range $n = 22$ (except as noted)
head-and-body length (HB)			
66 ± 5	69	—	69 ± 4
56-79			60-77
			($n = 23$)
tail length (TL)			
29 ± 3	27	21	29 ± 3
20-34			22-33
			($n = 23$)
condylobasal length (CBL)			
18.1 ± 0.5	20.3	19.2	19.4 ± 0.4
16.9-19.3			18.7-20.0
($n = 37$)			($n = 16$)
cranial breadth (CB)			
9.0 ± 0.2	10.4	9.4	9.5 ± 0.2
8.6-9.5			9.2-10.0
($n = 31$)			($n = 17$)
breadth of zygomatic plate (ZP)			
1.9 ± 0.2	2.5	2.1	2.3 ± 0.2
1.7-2.2			2.0-2.6
interorbital breadth (IO)			
4.2 ± 0.2	4.8	4.7	4.7 ± 0.1
3.9-4.7			4.4-4.9
breadth across first unicuspids (U1B)			
2.3 ± 0.1	3.2	2.6	2.6 ± 0.2
2.1-2.5			2.1-2.8
breadth across third unicuspids (U3B)			
2.7 ± 0.1	3.5	3.1	3.0 ± 0.1
2.4-3.0			2.7-3.3
breadth across second molars (M2B)			
5.3 ± 0.2	6.3	6.0	5.8 ± 0.2
4.9-5.6			5.2-6.2
palatal length (PL)			
7.7 ± 0.3	9.3	8.3	8.4 ± 0.3
7.1-8.6			7.9-8.9
length of upper toothrow (TR)			
6.9 ± 0.2	8.1	7.7	7.3 ± 0.2
6.3-7.3			6.8-7.7
length of unicuspid toothrow (UTR)			
2.3 ± 0.1	2.6	2.4	2.5 ± 0.1
2.0-2.5			2.2-2.7
length of molariform toothrow (MTR)			
5.1 ± 0.2	5.9	5.6	5.3 ± 0.1
4.8-5.6			5.1-5.5
			($n = 10$)
posterior width of M1 (WM1)			
1.7 ± 0.1	2.1	1.8	1.9 ± 0.1
1.5-1.8			1.7-2.0
length of mandible (ML)			
6.1 ± 0.2	7.5	6.3	6.5 ± 0.3
5.5-6.6			5.8-7.2

TABLE 1. Continued.

Cryptotis nigrescens (Monteverde) n = 41 (except as noted)	Cryptotis merriami		
	Monteverde	Finca San Bosco	Main geographic range n = 22 (except as noted)
height of coronoid process (HCP)			
4.3 ± 0.2	5.4	4.7	5.0 ± 0.2
3.9-4.7			4.5-5.3
(n = 40)			
height of coronoid valley (HCV)			
2.6 ± 0.2	3.1	2.8	2.9 ± 0.2
2.3-2.9			2.4-3.3
(n = 40)			
height of articular condyle (HAC)			
3.6 ± 0.2	4.3	3.7	3.8 ± 0.2
3.3-4.0			3.3-4.3
(n = 40)			
breadth of articular condyle (BAC)			
2.9 ± 0.1	3.5	3.2	3.0 ± 0.2
2.6-3.1			2.6-3.2
articular condyle to M3 (AC3)			
4.4 ± 0.2	5.3	4.7	4.6 ± 0.2
4.0-4.8			4.3-4.9
length of lower toothrow (TRD)			
5.4 ± 0.2	6.4	5.9	5.7 ± 0.2
5.1-5.8			5.3-5.9
length of lower molariform toothrow (m13)			
4.1 ± 0.1	4.9	4.5	4.3 ± 0.2
3.9-4.4			4.1-4.6
length of m1 (m1L)			
1.7 ± 0.1	2.1	1.8	1.8 ± 0.1
1.6-1.8			1.7-1.9
weight			
5.4 ± 1.0	7.8	—	—
3.0-7.5			
(n = 38)			

its presence in Costa Rica was based on a single specimen from Finca San Bosco (Fig. 1), near Tilarán (Woodman and Timm, 1993). The two species are relatively easy to distinguish: C. merriami is larger than typical Costa Rican C. nigrescens, and it has a more robust skull (particularly the mandibles); bulbous dentition (sensu Choate, 1970); a ventral branch of the sinus canal and associated foramen (see Woodman and Timm, 1999); no foramen dorsal to the dorsal articular facet; and a tendency toward only a single, large dorsal foramen. Cryptotis nigrescens and C. merriami were not thought to come into geographic contact.

I studied specimens in the Museo Nacional de Costa Rica, including recently-collected, unidentified shrews. Among these was a specimen of Cryptotis merriami (MNCR 358) from Monteverde (Fig. 1) that represents the second record of the species from Costa Rica. The Monteverde specimen was found dead along the Chomogo Trail (10°18′05″N, 84°47′27″W) in the Monteverde Cloud Forest Reserve on 14 June 1994. This trail extends from above 1550 m to just below 1700 m, running entirely through cloud forest. Collecting in the community of Monteverde, the reserve, and the surrounding area by biologists and local residents has yielded more than 70 Cryptotis in various museum collections—the largest collection of shrews from any locality in Central America. These specimens include 70 C. nigrescens, the new specimen of C. merriami, and one specimen of an unde-
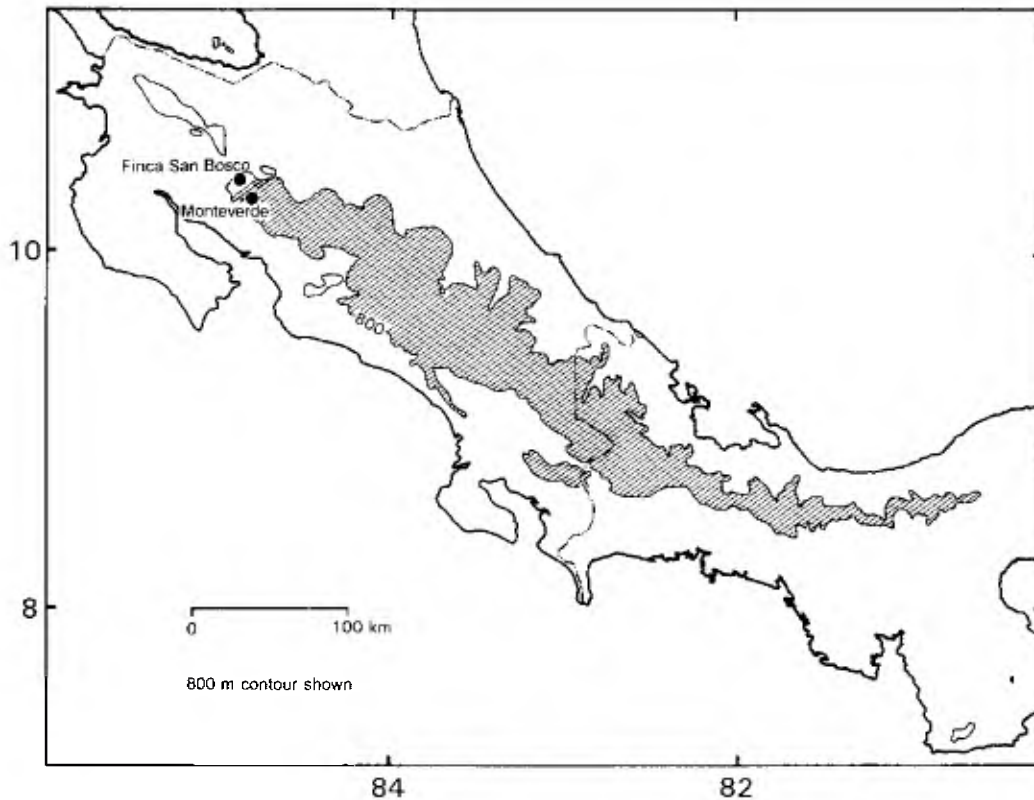
FIG. 1. Map of Costa Rica and western Panama showing the distribution of *Cryptotis nigrescens* (inferred from Woodman and Timm, 1993) and the locations of Finca San Bosco and Monteverde.

scribed, endemic form (*Cryptotis* sp. "a") probably related to *Cryptotis gracilis* Miller and *Cryptotis endersi* Setzer in Choate's (1970) group of "relict species." The numerically dominant *C. nigrescens* has been found in a variety of habitats from 870-1760 m, including cloud forest along the Chomogo Trail.

The new specimen of *C. merriami* confirms the presence of the species in the Tilarán Cordillera, extends the known distribution of *C. merriami* ca. 25 km to the south, and provides the first certain record of syntopy between *C. merriami* and *C. nigrescens*. Detailed examination of the Monteverde specimen indicates that it is within the range of variation for *C. merriami* in external measurements and in most nonmensural cranial and dental characters. The skull of this individual, however, is very large, measuring beyond the upper extremes of most cranial variables docu-

mented for other members of the species (Table 1) and for the *C. nigrescens*-group in general (see Woodman and Timm, 1993: Table 4).

The purpose of this paper is to review morphometrical variation within *C. merriami* and *C. nigrescens* and examine the possibility that the large *C. merriami* at Monteverde may represent a case of character displacement in the presence of a closely-related species.

METHODS

Terminology of dentition and dental characteristics follows Choate (1970). All measurements are in mm and follow Woodman and Timm (1993, 1999) and Woodman (1995); abbreviations are explained in Table 1. Skull measurements were taken to the nearest 0.1 mm using ei-

TABLE 2. Factor loadings for the first two factor axes from principal components analysis of nine cranial variables from *C. merriami* and Monteverde *C. nigrescens*. Abbreviations as in Table 1.

Variable	Factor 1	Factor 2
UTR	−0.281	0.761
ZP	−0.304	−0.440
IO	−0.329	−0.281
WM1	−0.332	0.072
TR	−0.337	0.320
PL	−0.348	−0.031
U3B	−0.351	−0.118
U1B	−0.355	−0.049
M2B	−0.355	−0.159
eigenvalue:	6.9845	0.5983
proportion of dispersion explained:	0.776	0.066

ther an ocular micrometer in a binocular microscope or a hand-held dial caliper. Standard external measurements are those recorded by the collector.

Principal components analyses (PCAs) and regressions were carried out using Minitab Release 8. Orthogonal principal components were calculated from the correlation matrix of nine untransformed cranial variables (ZP, IO, U1B, U3B, M2B, PL, TR, UTR, WM1). An initial PCA to evaluate the overall similarity of the Monteverde specimen with *C. merriami* and *C. nigrescens* included 24 *C. merriami* from throughout the species' geographic range (including Monteverde) and 41 *C. nigrescens* from Monteverde (Table 2, Fig. 2). To test for clinal variation in size, I regressed "size" on
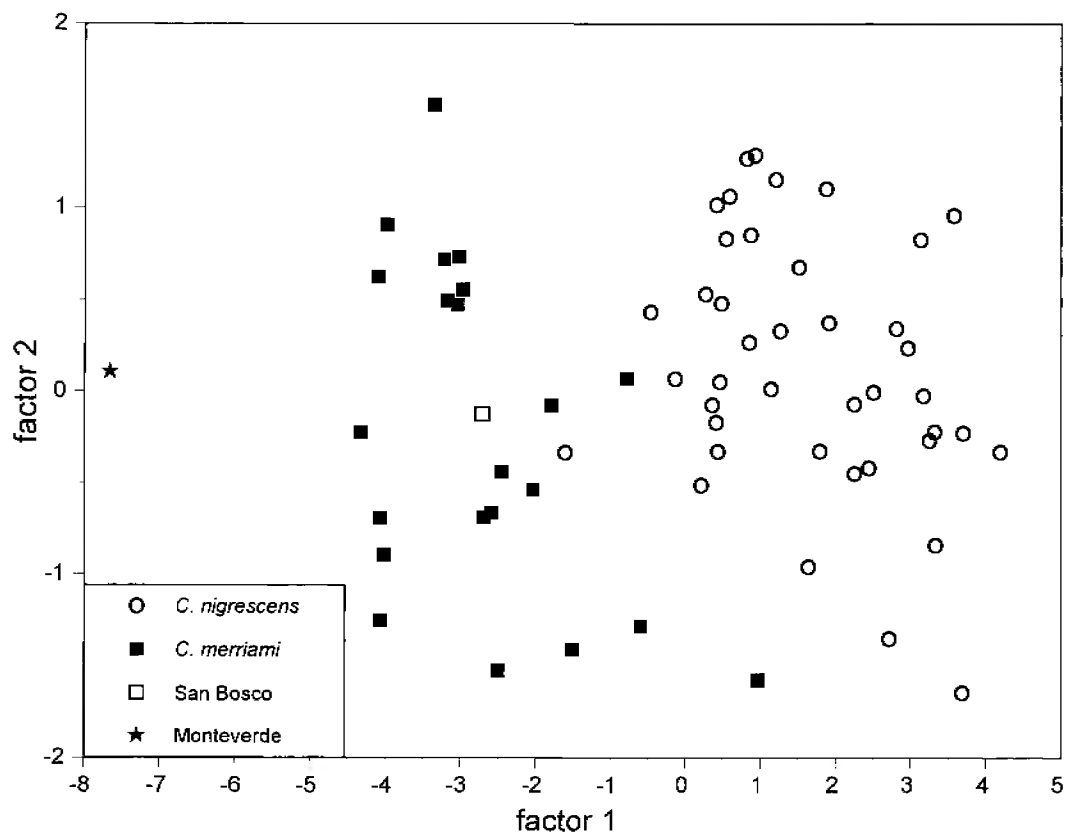

FIG. 2. Plot of factor scores from principal components analysis of nine cranial variables from *Cryptotis merriami* and *C. nigrescens*. The first factor axis represents overall size; because factor loadings are negative, the largest specimens have the lowest scores on this axis (Table 2). The second axis represents length-of-unicuspid-toothrow and length-of-upper-toothrow contrasted with breadth-of-zygomatic-plate and interorbital-breadth. The two axes account for 85% of the variation.

"geographic locality" individually for each species (Figs. 3, 4). For *C. merriami*, I used 23 specimens from throughout its geographic range (excluding the Monteverde specimen) to calculate the regression. For *C. nigrescens*, I used 49 specimens from Costa Rica and 33 from Panama. Each individual was treated as an single point in the regressions, although there may be a lack of independence among individuals from the same locality. "Size" in both regressions is represented by scores on the first factor axes of two PCAs carried out individually on *C. nigrescens* and on *C. merriami* (Table 3). "Geographic locality" is represented by scores on the first factor axis of a PCA of the untransformed decimal equivalents of the latitude and longitude for all collecting lo-

calities (Table 4). Latitude and longitude loaded equally (latitude = 0.707; longitude = 0.707) on the first factor axis, which accounted for 98.6% of variation. Factor 1 scores therefore describe the relative geographic position of each locality.

Specimens used in this study are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Escuela Nacional de Ciencias Biológicas, México City (ENCB); Field Museum, Chicago (FMNH); University of Kansas Natural History Museum, Lawrence (KU); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); James Ford Bell Museum of Natural History, St. Paul
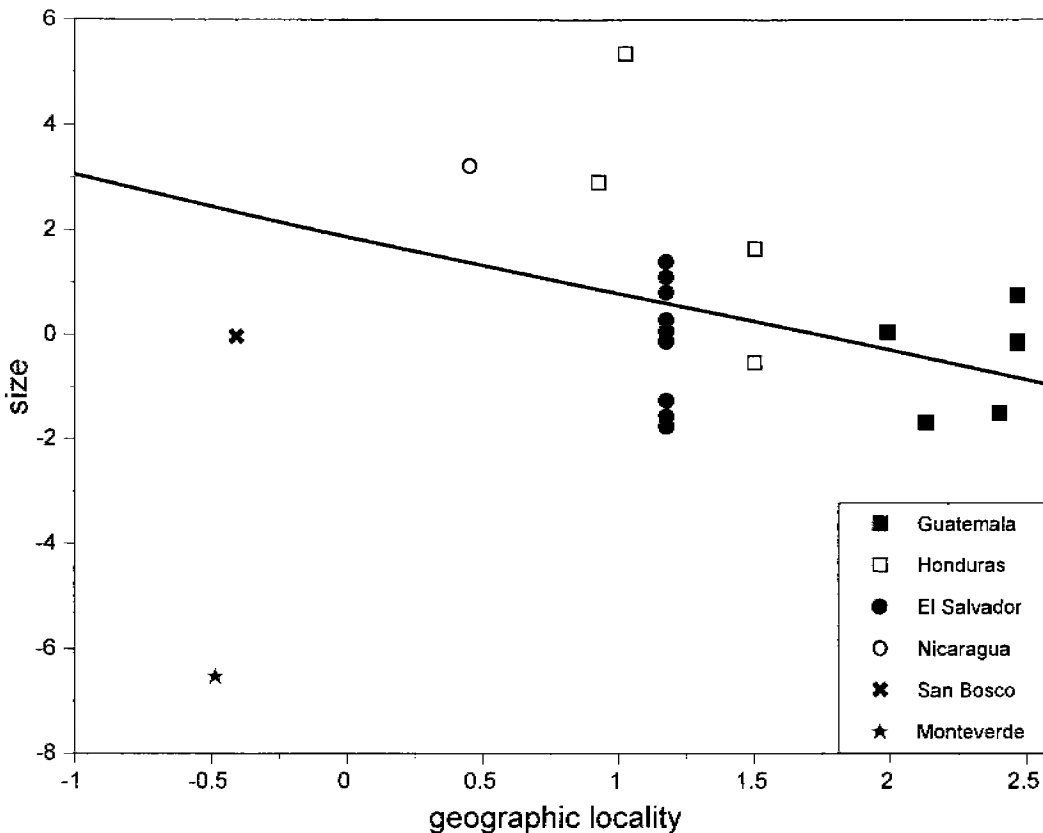

FIG. 3. Regression of factor 1 scores ("size") from principal components analysis of nine cranial variables against "geographic locality" for *C. merriami*. "Size" factor scores are negative, so that the smallest individuals have the largest positive scores (Table 3). "Geographic locality" is a factor score derived from a PCA of latitude and longitude for collecting localities (Table 4). The regression ($y = 1.32 - 0.742x$) is not significantly different from zero ($F = 1.92$, $P = 0.180$, adjusted $R^2 = 4.0\%$), indicating no recognizable geographic trends in size.
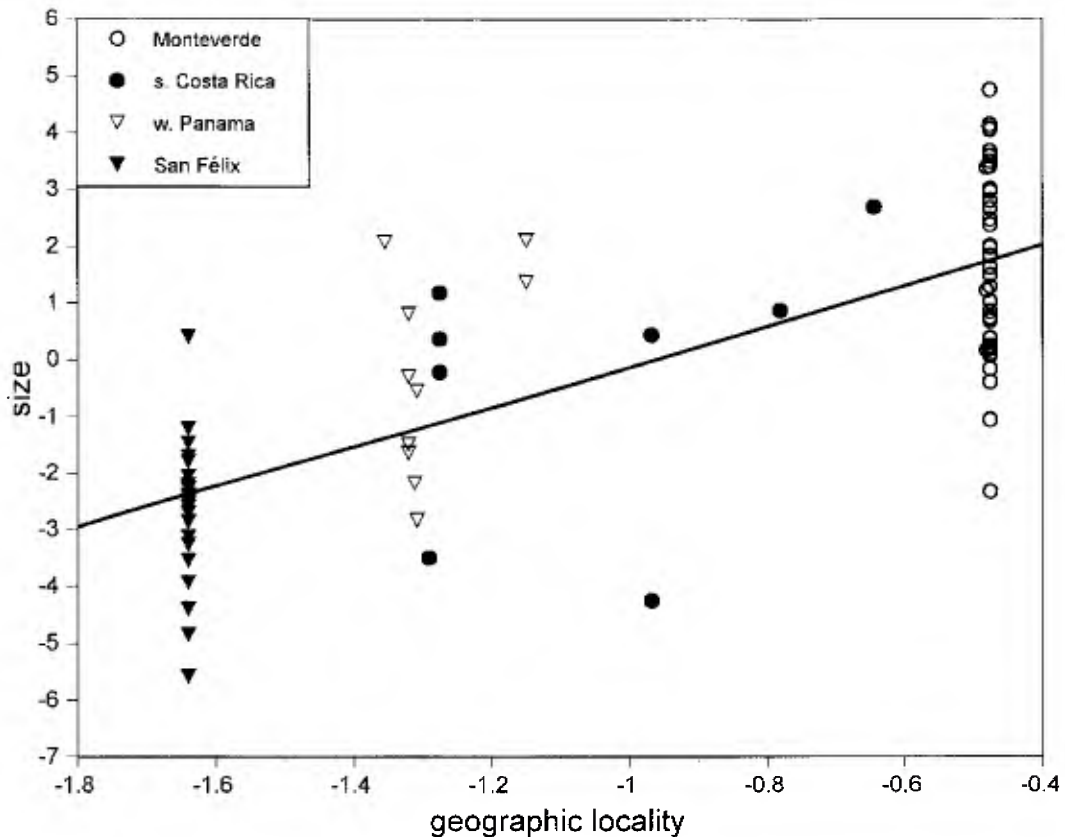
FIG. 4. Regression of factor 1 scores ("size") from a PCA of nine cranial variables against "geographic locality" for *C. nigrescens* in Costa Rica and Panama. The regression ($y = 3.39 + 3.55x$) indicates a significant trend of increasing size from northern Costa Rica through western Panama ($F = 103.21$, $P < 0.001$, adjusted $R^2 = 55.8\%$). Specimens listed as "s. Costa Rica" are from Costa Rican localities south of Monteverde; those from "w. Panama" are from west of San Félix.

(MMNH); Museo Nacional de Costa Rica, San José (MNCR); University of California Museum of Vertebrate Zoology, Berkeley (MVZ); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Departamento de Biología, Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); U.S. National Museum of Natural History, Washington (USNM).

RESULTS

A plot (Fig. 2) of factor scores on the first two factor axes from the PCA of *C. merriami* and *C. nigrescens* indicates that the two species overlap broadly on the second factor axis (length-of-unicuspid-toothrow and length-of-upper-toothrow contrasted with breadth-of-zygomatic-plate and interorbital-breadth—Table 2). However, both species form distinct clusters with little overlap on the first factor axis, illustrating their clear distinction in overall size (Table 2). This analysis supports the impression of a strong size difference between the Monteverde *C. merriami* and all other known specimens of the species, including the other Costa Rican specimen from Finca San Bosco. The Monteverde specimen is the largest *C. merriami* documented.

The slope of the regression line from the test for clinal variation in *C. merriami* (Fig. 3) suggests a trend of decreasing size from north to south in Central America, the op-

TABLE 3. Factor loadings for the first factor axis from two separate principal components analyses of nine cranial variables from *C. merriami* and *C. nigrescens*, respectively. Abbreviations as in Table 1.

Variable	C. merriami	C. nigrescens
ZP	−0.120	−0.170
IO	−0.174	−0.347
UTR	−0.259	−0.264
WM1	−0.345	−0.319
PL	−0.372	−0.352
M2B	−0.378	−0.381
TR	−0.385	−0.370
U3B	−0.404	−0.363
U1B	−0.420	−0.377
eigenvalue:	4.8973	6.0330
proportion of dispersion explained:	0.544	0.670

posite of what a clinal model based on the large size of the Monteverde specimen would predict. However, the slope is not statistically different from zero, and it explains only a small percentage of the variation ($F = 1.92$, $p = 0.180$, $d.f. = 22$, adjusted $R^2 = 4.5\%$), indicating little geographic variation in size. The second smallest individual in the analysis is from Nicaragua, which neighbors Costa Rica to the north. The Finca San Bosco specimen—the only other specimen of *C. merriami* from Costa Rica—is average size for the species (first factor axis coordinate = 0.05364). In contrast, the individual from Monteverde, the only locality where the species occurs in sympatry with *C. nigrescens*, is considerably

TABLE 4. Approximate latitude and longitude for collection localities of *C. merriami* and *C. nigrescens*. The factor score for each locality is from the first factor axis of a principal component analysis of all pairs of coordinates (see text). Geographic coordinates derive from gazeteers published by the United States Board on Geographic Names, from maps of the regions, and from original specimen tags.

Locality	Latitude	Longitude	Factor score
Guatemala:			
Jacaltenango	15°40′	91°44′	2.47670
Barillas	15°48′	91°18′	2.41113
San Pedro Carchá	15°29′	90°29′	2.14180
Tucurú	15°18′	90°04′	2.00206
Honduras:			
San José de Colinas	14°59′	88°18′	1.51491
Las Flores	14°40′	88°38′	1.51182
San Juancito	14°13′	87°04′	1.03979
Montaña de Monserrat	13°56′	86°57′	0.93859
El Salvador:			
Cerro Cacaguatique	13°46′	88°13′	1.18915
Nicaragua:			
Santa María de Ostuma	12°57′	85°58′	0.46491
Costa Rica:			
Tilarán	10°28′	84°58′	−0.39446
Monteverde	10°18′	84°47′	−0.47204
San Luis	10°17′	84°47′	−0.47712
Cinchona	10°13′	84°11′	−0.63912
Volcán Irazú	9°59′	83°51′	−0.77576
San Isidro del General	9°23′	83°42′	−0.96259
San Vito	8°50′	82°58′	−1.26971
Las Tablas	8°57′	82°46′	−1.28508
Panama:			
Volcán de Chiriquí	8°48′	83°33′	−1.14434
Fish Camp	8°58′	82°40′	−1.30293
19 km NNW El Volcán	8°56′	82°42′	−1.30621
Finca Santa Clara	8°51′	82°45′	−1.31507
Cerro Punta	8°52′	82°35′	−1.34897
Hato del Volcán	8°46′	82°38′	−1.36291
23 to 25 km NNE San Félix	8°27′	81°48′	−1.63453

larger than the range of size variation present throughout the geographic distribution of the species.

Woodman and Timm (1993) demonstrated that *C. nigrescens* at Monteverde is distinctly smaller than conspecifics from near San Félix, Panama, and suggested that *C. nigrescens* could be a complex of species. However, the plot of size (Fig. 4, Table 3) against geographic locality (Table 4) shows a gradual transition from populations of smaller individuals in northern Costa Rica to populations of larger individuals in western Panama. Regression analysis supports this trend ($y = 3.39 + 3.55x$; $F = 103.21$, $p < 0.001$, $d.f. = 81$, adjusted $R^2 = 55.8\%$). Rather than representing different taxa, *C. nigrescens* from Monteverde and San Félix represent two extremes of a gradual size cline.

DISCUSSION

Throughout its distribution, *C. merriami* exhibits no regular pattern of geographical variation in size, indicating that clinal variation does not account for the extremely large size of the Monteverde specimen. One possibility is that the Monteverde specimen represents an undescribed species closely related to *C. merriami*. However, in that case, the same suite of characters that supports its conspecificity with *C. merriami* would indicate that the two "species" are sister taxa, and the original question remains—why is the Monteverde specimen so big?

Environmental conditions at Monteverde and near Finca San Bosco, ca. 25 km to the north, are similar, and they certainly differ less than between northern Costa Rica and anywhere else in the geographic range of *C. merriami*. The one environmental variable that is most obviously different at Monteverde is the presence of *C. nigrescens*. It seems likely that the large size of *C. merriami* at Monteverde represents character displacement (Brown and Wilson, 1956) to facilitate coexistence by minimizing competition with *C. nigrescens*.

Character displacement has been documented in a number of mammals, including insectivores. Choate (1970:238) observed that *Cryptotis peregrina* and *Cryptotis goldmani* from Oaxaca, Mexico, were easier to distinguish where the two species lived in sympatry than where they occurred alone. In northern Europe, Malmquist (1985) showed that the European pygmy shrew, *Sorex minutus*, averaged significantly smaller in regions where it was sympatric with the European common shrew, *Sorex araneus*, than in regions where it existed alone. In contrast, the common shrew exhibited no differences between regions where it was sympatric with *S. minutus* and regions where the pygmy shrew was absent. The lack of character displacement in *S. araneus* is similar to the lack of size displacement in *C. nigrescens* at Monteverde.

The smaller size of *C. nigrescens* at Monteverde is part of a gradual trend of decreasing size from western Panama through northern Costa Rica (Fig. 4). But, if larger size is an adaptation that evolved in *C. merriami* to reduce competition with *C. nigrescens* at Monteverde, then why does *C. nigrescens* show no corresponding response (further diminution in size) to the presence of *C. merriami*? In Europe, the lack of morphological response in *S. araneus* was attributed to the low abundance of *S. minutus* in areas of sympatry and hence, the exposure of *S. araneus* "to only a weak interspecific competitive pressure" (Malmquist, 1985:375). A corresponding situation may exist at Monteverde, where the numerically dominant *C. nigrescens* has remained unchanged, and the less abundant *C. merriami* exhibits a distinct increase in size. Larger size allows predators to utilize prey sizes unavailable to smaller predators, whereas smaller size less typically bestows a trophic advantage (Wilson, 1975). However, Dickman (1988) argued that size variation in insectivorous mammals does not permit specialization on different sizes of prey. He hypothesized that larger insectivorous species can partly exclude smaller insectivores from microhabitats where large prey are more abundant. If the larger size of *C. merriami* permits assymetrical competition favoring its occurrence at Monteverde, it would be maladaptive for *C. nigrescens* to evolve smaller size.

Several studies have attempted to determine how much of a size difference is required for two members of the same trophic guild to coexist. In general, magnitudes of difference show great variability, depending upon what taxa and what measurements are considered. Hutchinson (1959) suggested that sympatry would require a two-fold difference in mass, which he equated to a size difference ratio of approximately 1.3 (range = 1.1-1.4), with size represented for mammals by length of skull. Similar ratios have been reported among Israeli canids (Dayan et al., 1992) and Miocene hyaenas (Werdelin, 1996), based on carnassial lengths. Sympatric gerbillid rodents exhibit size ratios ranging from 1.0 to 1.3 (Yom-Tov, 1991), whereas, a size ratio of 1.6 may be the norm among folivorous mammals (Maiorana, 1990).

Malmquist (1985) used the minimum distance between the upper second molars to investigate character displacement in *Sorex minutus* and *S. araneus*. The size ratio for this character in sympatry (1.4) was larger than in allopatry (1.3). Using a similar trophic measurement, breadth-across-upper-second-molars (Table 1), I determined the size ratio between *C. nigrescens* and typical *C. merriami* is 1.1, whereas the difference between *C. nigrescens* and the Monteverde specimen of *C. merriami* is 1.2—an increase in magnitude equivalent to that of the European shrews.

Unlike the European soricid community (Malmquist, 1985), the Monteverde community includes a third shrew, *Cryptotis* sp. "a"—a rare species more closely related to *C. gracilis* and *C. endersi* than to *C. nigrescens* or *C. merriami*. Using breadth-across-upper-second-molars (5.8 mm), *Cryptotis* sp. "a" is equal in size to typical *C. merriami* (Table 1) and is intermediate between *C. nigrescens* and *C. merriami* from Monteverde. The size ratios between *Cryptotis* sp. "a" and *C. nigrescens*, and between *Cryptotis* sp. "a" and *C. merriami*, are both 1.1. Hence, the larger size of *C. merriami* at Monteverde may be a response to the presence of an abundant sister species (*C. nigrescens*), the presence of an unrelated shrew the size of more typical *C. merriami* (*Cryptotis* sp. "a"), or, most likely, the presence of both species.

Fox and Kirkland (1992; see also Kirkland, 1991) suggested that an assemblage rule, initially formulated for Australian small mammals, may apply to communities of forest-dwelling shrews in eastern North America. This rule predicts that community assembly proceeds by functional groups (i.e., size groups) and that each such group should be represented by a single member before a second member of a functional group can be added. The functioning of this assemblage rule for insectivores presumably is enforced by competition for distinct classes of prey (e.g., Churchfield, 1991), although it may be brought about through interference competition (Dickman, 1988) or another form of coarse-grained habitat partitioning (Kirkland, 1991; Churchfield, 1991). If a similar assemblage rule functions in Central American forests, it would preclude the co-occurrence of similarly-sized species of shrews and should promote character displacement in size, as seen in *C. merriami* at Monteverde. The functioning of such an assemblage rule could be tested by closely examining where and on what different species in the community are feeding throughout the year.

Although the Costa Rican fauna has been intensely studied, large gaps remain in our knowledge of the region's mammals. Particularly little is known regarding the distribution and ecology of the region's smallest terrestrial mammals, the shrews. As predators of insects and other important soil- and plant-inhabiting invertebrates, shrews may play a crucial role in Neotropical systems. Their role may be better defined through additional study of the composition of soricid communities in tropical habitats and the interactions of community members.

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LITERATURE CITED

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