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SIZE EVOLUTION IN GOODWIN'S SMALL-EARED SHREW, *CRYPTOTIS GOODWINI* (MAMMALIA: SORICOMORPHA: SORICIDAE)

NEAL WOODMAN

ABSTRACT

Fossils of *Cryptotis goodwini* from Honduras indicate that body sizes of modern individuals average at least 18% larger than among members of the late Pleistocene population of this species. Palynological and other paleoenvironmental studies provide evidence that the Neotropical montane environments that these shrews inhabit were cooler and drier in the late Pleistocene than at present and supported communities of plants without modern analog. Therefore, the most likely cause of this change in size ultimately was related to climatic change at the end of the Pleistocene—but to what specific factors did the species respond? I examined the

possibilities that this species changed in size: to accommodate a change in temperature regime; to escape from predators; as a response to a change in intensity of interspecific competition; to take advantage of a newly abundant food resource. Based on evidence from studies of modern communities of shrews and niche partitioning, I hypothesized that size evolution in *C. goodwini* was directly related to changes in the community of soil and soil-surface invertebrates upon which the species depends, specifically an increase in the availability of earthworms (Annelida).

INTRODUCTION

The body size of an organism has significant implications for its life history traits, whether it be plant, ectotherm, or endotherm (Brown, 1995). Body size is significantly correlated with a host of morphological, physiological, ecological, and behavioral characteristics (Brown, 1995; Peters, 1983), and it has ecological and evolutionary consequences that impact individuals, populations, communities, and phyletic lineages (Brown and Maurer, 1986). Among animals, heritability of body size is variable, but tends to be high and consequently, subject to natural selection (Atchley et al., 1984; Leamy, 1988; Brown, 1995; Anderson and Handley, 2002).

Body size in both lineages and individual species has been shown to vary across different time scales. Direction of body size change also varies, even within the same lineage. For example, Cope's rule describes the observation that evolutionary lineages of animals tend to increase in size across geological time (LaBarbera, 1986; Jablonski, 1996). Some lineages, however, show the reverse trend toward decreased body size (Boucot, 1976). Lineages of living and recently extinct mammals tracked through the Quaternary exhibit both increases and decreases in

body size that in some instances appear to correspond to fluctuations between glacial and interglacial conditions (Kurtén, 1960, 1968; Nelson and Semken, 1970). More dramatic was the rapid size change of some mammal species at the end of the Pleistocene (Seymour, 1993; Martin 1996), coincident with the extinction of the North American Pleistocene megafauna (Guilday et al., 1964; Lundelius et al., 1983; Martin 1996). Size variation associated with climatic change also has been documented during the Holocene (Purdue, 1989; Purdue and Reitz, 1993).

Explanations for size changes in species of Quaternary mammals often involve poorly resolved responses to climatic change, especially change in global temperature regimes (Kurtén, 1960; Guilday et al., 1964; Lundelius et al., 1983). More specific responses include decreased body size to reduce heat stress in response to warmer temperatures (Smith et al., 1995) and decreased size in response to reduced availability of summer forage resulting from lower rainfall (Purdue and Reitz, 1993). Alternative explanations for size change include

Table 1. – Measurements in mm of fossil and modern *Cryptotis goodwini*. Statistics presented are mean \pm S.D. and observed extremes. Percent increase is the difference between the statistical means of the two samples.

Variable	Fossil ($n = 7$) ^a	Modern ($n = 32$) ^a	Percent increase
length-of-mandible	6.0 \pm 0.2 5.7–6.3	6.6 \pm 0.2 6.2–7.2	10.0%
height-of-coronoid-process	4.6 \pm 0.1 4.3–4.7	4.8 \pm 0.2 4.6–5.3	4.3%
height-of-coronoid-valley	2.8 \pm 0.1 2.7–3.0	3.0 \pm 0.1 2.8–3.4	7.4%
height-of-articular-condyle	3.8 \pm 0.1 3.6–3.9	4.2 \pm 0.2 3.8–4.8	10.5%
articular-condyle-to-m3	4.8 \pm 0.1 4.7–5.0 ($n = 5$)	5.5 \pm 0.2 5.0–5.9	14.6%
length-of-toothrow	5.8, 5.9 ($n = 2$)	6.4 \pm 0.2 5.9–6.8	6.4%
length-from-m1-to-m3	4.4 \pm 0.1 4.4–4.6 ($n = 5$)	4.7 \pm 0.1 4.4–4.9 ($n = 31$)	6.8%
length-of-m1	1.9 \pm 0.1 1.8–1.9	1.9 \pm 0.1 1.8–2.1	0%
breadth-of-articular-condyle	2.9 \pm 0.1 2.8–3.0	3.3 \pm 0.2 3.0–3.7	13.8%

^a except as noted

selective culling by human hunters (Goodwin, 1993; Flannery, 1995; Martin, 1996), resource limitation resulting from isolation on continental islands formed by rising sea level (Anderson and Handley, 2002; McFarlane et al., 1998), and interspecific competition within feeding guilds (Maiorana, 1990; Dayan et al., 1993).

Recently, Darin A. Croft and I identified remains of Goodwin's small-eared shrew, *Cryptotis goodwini*, from a late Pleistocene fossil site near Copán, Honduras. Modern *C. goodwini* has a discontinuous distribution in montane habitats above 1100 m in parts of southern Mexico, Guatemala, El Salvador, and Honduras. The areas in which this shrew lives are temperate in aspect, and the environment is dominated by cool, moist pine and mixed pine/broadleaf forests that may experience severe frosts (Woodman and Timm, 1999). *Cryptotis*

goodwini is one of the most derived members of the *C. goldmani*-group of small-eared shrews, a cohesive clade marked by apomorphic modifications of the forelimb that include lengthening and broadening of the foreclaws, shortening and broadening of the metacarpals, and extensive modification of the humerus—adaptations likely associated with enhanced digging through leaf litter or soil (Woodman and Timm, 1999). Study of fossil mandibles and humeri from the site indicate a large difference in size between late Pleistocene and modern populations of *C. goodwini*. It is the purpose of this paper to substantiate and quantify these differences in size and to present a hypothesis regarding the reasons for change in size based on what is known about such variation in small mammals and in soricomorphs in particular.

METHODS

Information regarding fossils from near Copán, western Honduras, are from unpublished data in a report prepared from by Darin A. Croft and me,

which has been submitted for publication elsewhere. The site is a cave originally excavated in the 1940's by an expedition from The Field

Table 2. – Factor scores on the first two axes from PCA of modern and fossil *Cryptotis goodwini*. Variables are listed in ascending order based on PC I score.

Variable	PC I	PC II
height-of-articular-condyle	-0.473	-0.013
length-of-mandible	-0.456	-0.115
breadth-of-articular-condyle	-0.443	0.066
height-of-coronoid-valley	-0.411	0.230
height-of-coronoid-process	-0.421	0.208
length-of-m1	-0.163	-0.941
eigenvalue:	4.1497	0.9753
proportion of variation explained:	69.2%	16.3%

Museum, Chicago, Illinois. Preservation and types of remains suggest that the accumulation of bone in the cave resulted mostly from the work of avian predators. Among the recovered remains of small mammals were complete and partial mandibles, maxillae, and postcranial bones of small-eared shrews that we were able to identify based on suites of characters (Woodman, 1996, 2002; Woodman and Timm, 1992, 1993, 1999, 2000) and by direct comparison with modern specimens of North, Central, and South American species. All remains of shrews are referable to three Recent species (*Cryptotis orophila*, *Cryptotis merriami*, and *C. goodwini*) that currently inhabit Honduras (Woodman and Timm, 1992).

Mandibular measurements used in comparisons of fossil and modern *C. goodwini* follow Woodman (1995) and were recorded to the nearest 0.1 mm using an ocular micrometer in a binocular microscope (Table 1). All measurements are given in mm, weights in g. Fossils were compared to a sample of 34 modern *C. goodwini*; these have mean head-and-body length of 84 ± 5 mm and mean weight of 16.2 ± 1.8 g. To study the morphological relationships between fossil and modern *C. goodwini*, orthogonal principal components were calculated from the correlation matrix of six \log^{10} -transformed variables (Table 2) measured from 32 modern and seven fossil right mandibles of *C. goodwini*. The resulting scores were plotted on a graph of the first principal component axis (PC I), interpreted as representing overall size (Table 1), vs. the second axis (PC II), representing length of first lower molar (Fig. 1). To further investigate size relationships

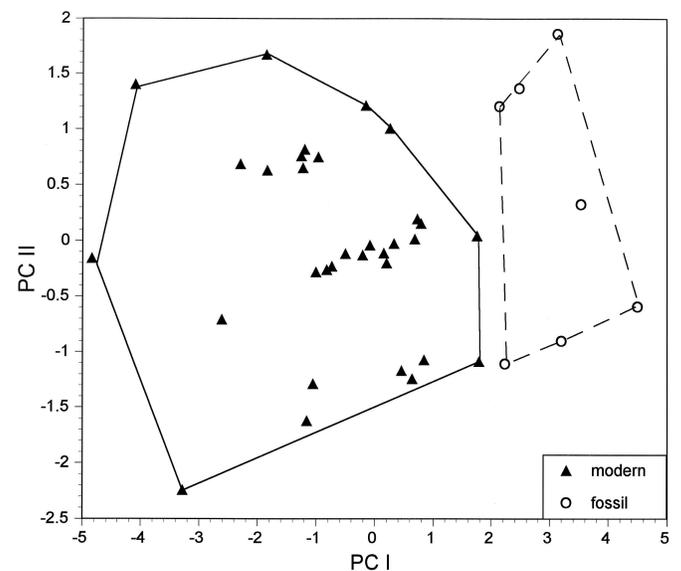


Fig. 1. – Plot of factor scores on first two factor axes from PCA of six variables from modern (\blacktriangle) and fossil (\circ) *Cryptotis goodwini*. Factor loadings on PC I are negative (Table 1), so the most negative scores represent the largest individuals.

between the two samples, I regressed height-of-coronoid-process on length-of-mandible for the modern specimens (Fig. 2). I then overlaid the fossil specimens on the plot to determine visually their relationship to the regression line.

I determined the magnitude of size change between the fossil and modern samples of *C. goodwini* by calculating a percentage increase using the following expression:

$$\left(\frac{(\text{modern sample}) \times 100}{(\text{fossil sample})} \right) - 100$$

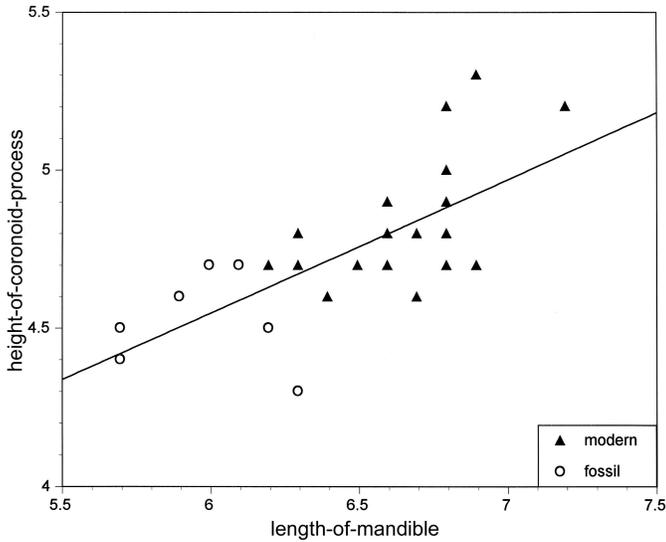


Fig. 2. – Plot of height-of-coronoid-process (HCP) on length-of-mandible (ML) for modern (▲) and fossil (○) *Cryptotis goodwini*. Regression was calculated using only the modern specimens [HCP = 1.99 + 0.426 (ML); $F = 15.88$; $P = 0.000^{***}$; adjusted $R^2 = 32.4\%$].

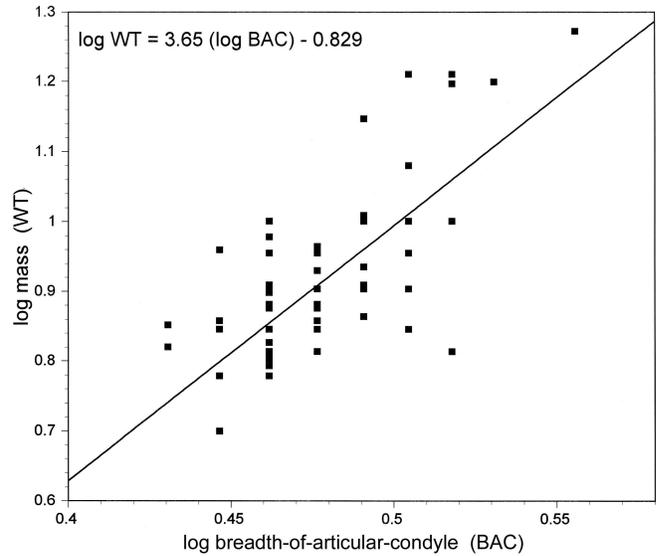


Fig. 3. – Plot of log mass on log breadth-of-articular-condyle for members of the *Cryptotis mexicana*-group. The resulting regression equation was used to predict mass for fossil *Cryptotis goodwini*.

Percentage size increase was calculated for each of the mandibular variables measured. However, these variables are difficult to compare directly with measures used in other studies or with modern populations of shrews. Because the ultimate goal was to estimate a common measure of body size, I calculated regression equations (Martin, 1990) to estimate mass and head-and-body length for the fossil specimens using correlated mandibular variables measured from all modern species of the *C. mexicana*-group. These shrews share a common evolutionary history with *C. goodwini* (Woodman and Timm, 1999) and should most accurately represent the different size morphs of *C. goodwini*. Among the mandibular variables, breadth-of-articular-condyle (BAC) had the highest correlation with mass (WT; $r = 0.739$), so I regressed log WT on log BAC using 75 specimens of six species to obtain an equation for estimating mass (Fig. 3). Mass is perhaps the most commonly accepted measure of mammalian body size, but weights generally are not available for most Central American specimens of *Cryptotis*. Head-and-body length provides a reasonable alternative measure of overall body size, and this measure is readily available from most museum specimens. Height-of-articular-condyle (HAC) had the highest correlation with head-and-body length

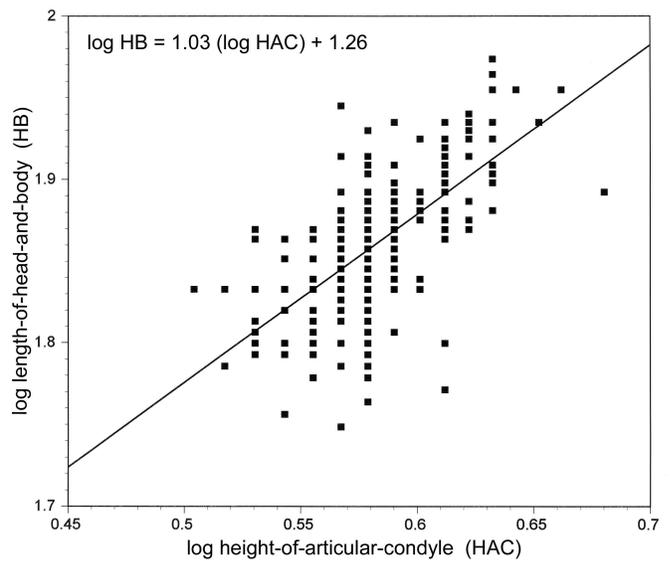


Fig. 4. – Plot of log head-and-body length on log height-of-articular-condyle for members of the *Cryptotis mexicana*-group. The resulting regression equation was used to predict head-and-body length for fossil *Cryptotis goodwini*.

(HB; $r = 0.655$), and I regressed log HB on log HAC using 222 specimens of ten taxa (*C. mexicana* provided two samples, one from Oaxaca, the other from Veracruz) (Fig. 4). The two regressions yielded the following equations for estimating body

size:

$$\log WT = 3.65 (\log BAC) - 0.829$$

adjusted $R^2 = 52.3\%$

$$\log HB = 1.03 (\log HAC) + 1.26$$

adjusted $R^2 = 40.8\%$

Although the equation for mass has a higher adjusted R^2 value, the plot of log WT on log BAC showed that the relationship between these variables is not linear, and the predictive ability of the equation would be particularly poor for larger individuals. The plot of log HB on log HAC shows a more linear relationship between these values, and the equation for head-and-body length probably has better predictive value overall.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BM); California Academy of Sciences, San Francisco (CAS); Colección Nacional de Mamíferos, Instituto de Biología, Universidad Na-

cional Autónoma de México, Mexico City (CNMA); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Department of Zoology, The Field Museum, Chicago (FMNH); Department of Geology, The Field Museum, Chicago (FMNH-PM); University of Kansas Natural History Museum, Lawrence (KU); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Comparative Zoology, Cambridge (MCZ); James Ford Bell Museum of Natural History, St. Paul (MMNH); Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City (MZFC); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF); Texas Cooperative Wildlife Collection, College Station (TCWC); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); National Museum of Natural History, Washington (USNM); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZMFK).

RESULTS

The plot of factor scores on the first two factor axes from PCA indicates no apparent shape differences between the fossil and modern samples (PC II; Table 1), but the two groups of specimens differ greatly in size (PC I). In this plot, all of the fossils are smaller than any of the modern specimens, with no overlap between the two groups (Fig. 1).

On the bivariate plot of height-of-coronoid-process (HCP) and length-of-mandible (ML), the fossils again plot much smaller than modern individuals, with little overlap between groups (Fig. 2). The regression calculated for the modern specimens describes a positive trend of increasing height-of-coronoid-process with increasing length-of-mandible [$HCP = 1.99 + 0.426 (ML)$; $F = 15.88$; $P = 0.000^{***}$; adjusted $R^2 = 32.4\%$]. Although much smaller in size, the fossils appear to conform to the trend established by the modern specimens, substantiating that a simple, yet significant, change in size has occurred in *C. goodwini*.

Fossil humeri of *C. goodwini* also were recovered from the Copán site. They are distinctly smaller

than humeri of modern *C. goodwini* (Fig. 5), and they support the contention of a distinct difference in size between the two populations. Humeri were not measured, however, owing to a paucity of complete specimens and the few modern reference specimens available.

The magnitude of the increase of *C. goodwini* from the late Pleistocene to the Holocene depends upon the variable measured and how it is interpreted. Among the individual mandibular variables I measured, the increase varied from 0% to 14.6% (Table 1). The largest univariate measurement, length-of-mandible, shows a 10% increase in size. The mean value of this measurement for the late Pleistocene population is most similar to that for modern *Cryptotis mexicana* from Oaxaca, which have a mean head-and-body length of 69 mm, and mean mass of 7.4 g. These values indicate a 22% increase in head-and-body length and a 119% increase in mass. The regression

equation for mass yielded an estimate for fossil *C. goodwini* of 6.9 ± 0.7 g (range, 6.4–8.2), approximately the size of modern *Cryptotis obscura* (mean head-and-body length = 66 mm; mean weight = 6.9 g). This calculation indicates a 27% increase head-and-body length and a 135% increase in mass. However, as noted previously, the relationship between mass and breadth-of-articular-condyle does not appear to be linear (Fig. 3), and mass estimated using this relationship may be inaccurate. The regression equation for head-and-body length yielded an estimate of 71 ± 2 mm (range, 68–74), indicating an 18% increase in size of modern *C. goodwini*. This estimate indicates a Pleistocene population of shrews about the size of modern *Cryptotis peregrina* (mean head-and-body length = 72; mass unknown).

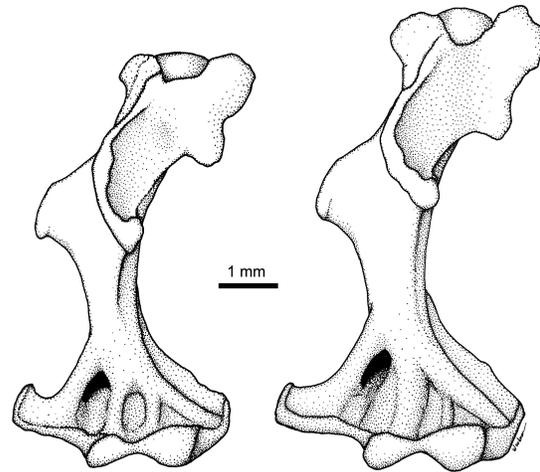


Fig. 5. – Fossil (left) and modern (right) humeri of *Cryptotis goodwini*.

DISCUSSION

PATTERNS OF BODY SIZE CHANGE AT THE END OF THE PLEISTOCENE

A number of species of mammals underwent changes in body size at the end of the last glacial. Typically, larger-bodied forms occupied mid- and late-glacial landscapes, whereas smaller-bodied forms replaced them in the Holocene (e.g., Martin, 1993, 1996; Goodwin, 1993; Guilday et al., 1964; Kurtén, 1968; Lundelius et al., 1983; Seymour, 1993; Smith et al., 1995). However, the response was not the same in magnitude or direction in all mammals. Guilday et al. (1964) reported six small mammals that exhibited a decrease in size varying from 1 to 9% from the late Pleistocene to the Holocene, and four that showed an increase of 5–13%. During approximately the same interval, jaguars (*Panthera onca*) decreased in size by 15% (Seymour, 1993), bushy-tailed woodrats (*Neotoma cinerea*) by 20% (Smith et al., 1995), and muskrats (*Ondatra zibethicus*) by 48% (Martin, 1993). The magnitudes of these changes are based on different measures and are not directly comparable. Nevertheless, there appears to be corroboration for a general tendency among mammals to decrease in body size at that time.

In contrast, lineages of North American soricids generally appear to have remained fairly static in size through time. Guilday et al. (1964) reported two species of shrews (not included among the ten spe-

cies previously mentioned) as being larger in the late Pleistocene than in the modern environment. *Sorex cinereus* underwent a 5% decrease in size at the end of the Wisconsin glacial epoch. *Blarina brevicauda* showed a gradual decrease in size from older to younger strata, but this trend was attributed to increased contamination of larger, fossil *B. b. brevicauda* by smaller, modern *B. b. kirtlandi* (Guilday et al., 1964), or by varying mixtures of up to three contemporaneous taxa of *Blarina* (Graham and Semken, 1976). In fact, Jones et al. (1984) found no substantial change in size in any species of *Blarina* during the last 2 million years. Similarly, *Cryptotis mayensis* from the Yucatan Peninsula showed no change in size during the transition from late Pleistocene to Holocene conditions (Woodman, 1995). It appears, therefore, that by increasing in size at the end of the Pleistocene, *C. goodwini* is anomalous both for mammals in general and relative to other North American soricids.

CLIMATIC CHANGE IN SOUTHERN NORTH AMERICA

With some exceptions (e.g., Goodwin, 1993; Martin, 1996), most changes in size of North American mammals at the end of the Pleistocene have been suggested to have occurred in response to large scale changes in climate that marked a transition to the Holocene (Lundelius et al., 1983).

Climatic change in northern North America at the end of the Pleistocene is well documented (Davis, 1976; Lundelius et al., 1983), however, the climatic regimes in Mexico and Central America are less well understood. Palynological and other paleoenvironmental studies indicate that Neotropical montane regions currently inhabited by *C. goodwini* were not left unaffected by Pleistocene climatic variations associated with northern hemisphere glaciation, as previously suspected. Alpine glaciers occurred on the highest peaks in Costa Rica (Hastenrath, 1973). During the full- and late-glacial, montane vegetation zones were 500–1000 m lower in Central America, and some plant species now separated by elevation overlapped in their distributions, resulting in communities without modern analog. Estimated mean annual temperatures for this region range from 4° to 8° C lower than at present, and montane environments were cooler and drier (Martin, 1964; Markgraf, 1989; Bush and Colinvaux, 1990; Bush et al., 1992; Leyden et al., 1993; Islebe and Hooghiemstra, 1997). The direct effects of such environmental changes on *C. goodwini* are unknown. Based on what we know of its modern distribution, however, it is likely that the late Pleistocene distribution of this species extended to lower elevations and was broader in geographic extent.

INTERPRETATIONS OF SIZE CHANGE

Traditionally, mammalian variation in size between glacial and interglacial environments had been interpreted in the context of classical understanding of Bergmann's rule, that endotherms increase in size with latitude because, by decreasing their surface-to-volume ratio, they save energy in cold environments (Mayr, 1963; McNab, 1971). The general explanation was that larger-bodied forms of a species with smaller surface-to-volume ratios were characteristic of colder Pleistocene climates, and smaller-bodied forms were typical of warmer Holocene climates (Guilday et al., 1964; Kurtén, 1968; Lundelius et al., 1983). This generalization fails on a number of points. First, although many mammals exhibit size variation with latitude, these patterns are not always linear, indicating that temperature alone is not the controlling variable (McNab, 1971; Boyce, 1978; Geist, 1987). Second, in detailed studies the factors responsible for the

variation that Bergmann's rule attempts to describe have proven to be much more varied and complex than a single response to either colder mean annual temperatures or greater extremes of cold (McNab, 1971; Boyce, 1978; Geist, 1987; Smith et al., 1995). Third, late Pleistocene environments in North America have been shown to have been less extreme and more equable rather than simply colder (Lundelius et al., 1983). Also, a Bergmann's response to colder temperatures does not explain why some mammals, including *C. goodwini*, increased in size after the end of the Pleistocene.

Studies of patterns of modern size variation in individual taxa have contributed valuable information regarding size variation through time (e.g., Purdue and Reitz, 1993; Smith et al., 1995). Many species of mammals exhibit regular clinal variation in size that corresponds to physical environmental factors (Boyce, 1978; Geist, 1987; Smith et al., 1995). Other species vary in size in response to changes in community structure and competitive interactions (Brown and Wilson, 1956; Yom-Tov, 1991). Many notable examples of size changes have been documented between mainland and island populations of mammal species (Heaney, 1978; Lomolino, 1984, 1985; Brown and Lomolino, 1998; Anderson and Handley, 2002).

Brown and Maurer (1986) outlined several ecological advantages for increased size in evolutionary lineages that also can be applied to species and to individuals. Larger individuals spend less energy per unit biomass, so they are more efficient at using food resources. Larger size also permits more efficient homeostasis and greater mobility, enabling individuals to tolerate a wide range of environmental conditions and seek more favorable habitats. Larger size can be advantageous in avoiding predators. Larger individuals often can exclude smaller competitors from preferred resources. I reworked these advantages into three general categories, that I used as a starting point for a discussion of body size variation in *Cryptotis goodwini*: response to a lower temperature regime during the late Pleistocene; escape from predation; and interspecific competition. In addition, I considered a fourth alternative, that size increase in *C. goodwini* provided the opportunity to exploit a new, abundant food resource.

1. Lower temperature regime

Soricines are active throughout the year even at the northernmost latitudes they inhabit. Contrary to what might be expected, rather than increasing mass prior to the cold season, individuals of species at high latitudes lose body mass in autumn and early winter, so they are smaller during the coldest parts of the year (Hyvärinen, 1984; Yaskin, 1984; Genoud, 1985; Merritt, 1995). This regular pattern of winter reduction in mass and size, known as Dehnel's phenomenon, is considered to be an adaptation to reduce overall energy requirements by reducing food requirements and foraging time during winter when food resources are more difficult to locate (Hyvärinen, 1984; Mezhzherin, 1964; McNab, 1991). In addition, some soricines exhibit a clinal variation in body size that manifests itself in three ways and at two taxonomic scales: (1) interspecifically—there is a tendency for the smallest species to occupy colder regions (Mezhzherin, 1964); (2) intraspecifically—populations of some species exhibit smaller mean body size in colder, more northern climates (Mezhzherin, 1964); (3) also intraspecifically—the magnitude of seasonal size reduction within a species also varies geographically, with the greatest decrease in the coldest climates (Hyvärinen, 1984; Mezhzherin, 1964; Pucek, 1970).

The general pattern among smaller soricines for dealing with extreme cold temperatures is to decrease overall demand for energy by shrinking in size (McNab, 1991), which is the opposite of the response predicted by Bergmann's rule. The primary demand is abundant food to fuel metabolism. Migration to new localities or more favorable microclimates either is not an issue for these shrews or is not impaired by this shrinkage. Whether these patterns apply to Neotropical montane *Cryptotis* as well as to northern *Sorex* is uncertain (McNab, 1991). Regardless, large size is not necessarily linked to lower temperature regimes in soricines.

2. Escape from predation

Common predators on shrews include a variety of mammals (e.g., Canidae, Felidae, Mustelidae), birds (e.g., Accipitridae, Tytonidae, Strigidae), and reptiles (Serpentes). The Honduran fossils appear to have been accumulated by owls. Although in-

formation on predation on modern and fossil shrews is incomplete, the increase in size of *C. goodwini* appears to have been insufficient to have had a large impact on its rate of predation. For example, in South America, barn owls (*Tyto alba*) prey on some of the largest members of the genus *Cryptotis* (Woodman, unpubl. data)

3. Competition

A number of lines of evidence suggest that interspecific competition can affect body sizes of shrews. As in other mammals (e.g., Maiorana, 1990; Werdelin, 1996; Yom-Tov, 1991; Dayan et al., 1992), some communities of sympatric soricines exhibit more or less evenly-spaced size distributions that have been interpreted to result from competition for food resources (Churchfield and Sheftel, 1994; Fox and Kirkland, 1992) following the ecological rule of limiting similarity (Hutchinson, 1959). Also, most insular populations of soricines correspond to the island rule (reformulated by Lomolino, 1985) and tend to average larger than conspecifics in the nearest mainland habitats (see Alexander, 1996; Hanski and Kuitunen, 1986; Lomolino, 1983, 1984). The generalized biogeographical explanation for increased size on islands is ecological release from competition (Lomolino, 1985; Brown and Lomolino, 1998), although predation and immigrant selection also may play important roles (Lomolino, 1984). However, some insular soricine and crocidurine shrews tend to be smaller than mainland conspecifics (Lomolino, 1983), suggesting the effects of resource limitation (Lomolino, 1985; Brown and Lomolino, 1998) rather than competition. Studies of the European shrews *Sorex araneus* and *Sorex minutus* more directly implicate competition as a primary contributing variable affecting size (Malmquist, 1985; Dickman, 1988; but see Hanski and Kuitunen, 1986). In areas where these two species are sympatric, the smaller species, *S. minutus*, is smaller than in areas where it occurs alone. However, *S. araneus* retains the same body size regardless of whether it is sympatric with the other species. In this case, differences in size may be advantageous only for the larger of the two sympatric species, either by permitting it physically to take a wider variety of prey (Churchfield and Sheftel, 1994) or by

promoting interference competition (Maiorana, 1978; Wilson, 1975; Dickman, 1988).

Alternatively, it has been shown, based on overlap in food resource use by sympatric soricids, that difference in body size dimensions alone maybe insufficient to achieve ecological separation and that differences in body size alone are not necessary to permit coexistence (Churchfield and Sheftel, 1994). Shrews are opportunistic feeders and, despite some specialization within multispecies communities of soricines, overlap in food resources can remain high (Churchfield, 1991; Churchfield and Sheftel, 1994).

One of the assumptions of these community-wide studies of competition is that interactions are strongest among mammalian species within the same taxonomic order or family. Provided that competition among shrews comes primarily from other shrews, it seems unlikely that this factor has had a strong influence on size in *C. goodwini*. Only three other soricid species currently occur in Honduras: *Cryptotis hondurensis* (mean head-and-body length = 61 mm; mass unknown; known elevational distribution 1680–1700 m); *Cryptotis merriami* (mean head-and-body length = 69 mm; mass unknown; 975–1650 m); and *Cryptotis orophila* (mean head-and-body length = 63 mm; mean mass = 5.8 g; 1150–1980 m). All three species are much smaller than modern *C. goodwini* (mean head-and-body length = 84 mm; mean mass = 16.2 g; 1100–3350 m), and they tend to occur at lower elevations, so interspecific interactions are limited in part by habitat preferences. Fossils of two of these species (*C. merriami* and *C. orophila*) were recovered with *C. goodwini* from near Copán. Their co-occurrence in the site may be a taphonomic artifact resulting from the foraging habits of the avian predators responsible for the accumulation of the remains. Alternatively, it may indicate that the distributions of these species were more syntopic in the late Pleistocene, and *C. goodwini* faced more competition at that time. Regardless, it seems unlikely that the largest species (fossil *C. goodwini*, mean head-and-body length = 71 mm; mean mass = 6.9 g) would respond to decreased competition in the Holocene by increasing its size.

4. New food resources: a hypothesis

Body size in sympatric terrestrial shrews reflects foraging mode. Larger species are soil foragers that tend to consume larger prey, such as earthworms, whereas smaller species tend to concentrate more on smaller, surface-dwelling invertebrates (Churchfield and Sheftel, 1994; see also Whitaker and Mumford, 1972; Butterfield et al., 1981; Whitaker and French, 1984; Rychlik and Jancewicz, 2002). Although larger size may reflect the physical requirements of feeding either on larger prey or deeper in the soil horizon (Churchfield and Sheftel, 1994), it also can promote competitive exclusion of smaller species (Dickman, 1988). In the absence of larger competitors, smaller shrews can increase in size (Malmquist, 1985) and take larger invertebrates as prey (Dickman, 1988). That body size in shrews can respond to availability of resources is suggested by Dehnel's phenomenon (Hyvärinen, 1984; Yaskin, 1984; Genoud, 1985; Merritt, 1995) and by distributional patterns of shrews in which larger species and larger individuals live in more southern areas, where resources are more abundant (Mezhzherin, 1964). Similarly, the increased size of insular soricines (see Alexander, 1996; Hanski and Kuitunen, 1986; Lomolino, 1983, 1984) has been attributed to the increase in resource availability associated with competitive release.

The larger body size of Holocene *C. goodwini* indicates that it is capable of foraging on larger soil invertebrates. Moreover, this foraging mode is consistent with modifications of its forearm that have been interpreted as adaptations for digging (Woodman and Timm, 1999). It also seems possible that resource availability—specifically the increased abundance of larger soil invertebrates in the Holocene—acted as a selective force for larger size in these shrews, or, more likely, acted to relax selection for smaller size. As noted previously, the late Pleistocene climate of montane Central America was cooler and drier, and species of plants were organized into communities without modern analogs (Bush and Colinvaux, 1990; Bush et al., 1992). Climatic changes associated with the end of the Pleistocene resulted in significant reorganization of plant communities and undoubtedly affected animal communities as well. I suggest that the smaller size of *C. goodwini* during the late Pleistocene was a con-

sequence of lowered availability of food resources resulting directly from the drier climate or the combination of drier and cooler conditions (Bush and Colinvaux, 1990; Islebe and Hooghiemstra, 1997; Leyden et al., 1993; Markgraf, 1989). These conditions, in turn, affected community membership and restricted the diversity and abundance of soil invertebrates on which these shrews feed, particularly during the season of least abundance.

Earthworms are one of the most common groups of soil macrofauna in tropical rain forest soils, averaging 51% of total biomass (Fragoso and Lavelle, 1992). Species of earthworms vary in their tolerances to environmental conditions. However, they have inefficient physical and physiological adaptations for water conservation, and most species are more active in moist than dry soils. Among tropical rain forest communities, density and biomass diminish with decreasing annual rainfall, from a peak at about 3000 mm (Fragoso and Lavelle, 1992). Earthworms can be driven deeper into the soil by seasonally dry or cold conditions, and they may enter resting stages or torpor (Lee, 1985; Edwards and Bohlen, 1996). Local density and biomass peak during the wet season and are at their lowest during the dry season, when earthworms migrate deeper into the soil horizon (Fragoso and Lavelle, 1992). Earthworms also are affected by changes in the vegetational community which alter the abundance and quality of their food (Edwards and Bohlen, 1996). Tropical and temperate regions are dominated by taxonomically distinct species of earthworms. Communities of northern temperate areas are composed mainly of species of Lumbricidae, a family that is rare in the tropics, except at high altitude (Lee, 1983). In contrast, Central American tropical rain forest communities are dominated by the Megascolecidae (tribes Acanthodrilini and Dichogastini—Fragoso and Lavelle, 1992).

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Cooler, drier conditions during the late Pleistocene may have resulted in lowered abundance and diversity and/or important changes in species membership of the earthworm community compared with the present. Reduced availability of an important food resource during that time may have caused *C. goodwini* to concentrate on a larger proportion of smaller invertebrates or to specialize on smaller, energy-rich items (e.g., insect larvae), thereby favoring selection for shrews of smaller body size. A similar decreased availability in earthworms resulting from late Pleistocene aridity has been postulated as a cause for the extinction of the long-beaked echidna, *Zaglossus*, on the Australian mainland (Griffiths, 1978). Increased humidity and associated vegetational changes accompanying the transition to Holocene conditions may have resulted in a modified prey resource that relaxed selection for smaller body size or even selected for increased size among *C. goodwini*. Although larger shrews require more food overall, they require less energy intake as a percentage of body size, and they can subsist more readily on lower quality food, if it is abundant (Rychlik and Jancewicz, 2002). Hence, larger size is a viable strategy when food resources are not limiting (Brown and Maurer, 1986; Hanski, 1994).

This hypothesis is based on assumptions that require testing and that define areas for further research. These include the ideas that earthworms provide an abundant preferred resource for soricines, and that Central American shrews, including *Cryptotis goodwini*, partition food resources by body size in a manner similar to North American and Eurasian soricines, with larger species taking a greater proportion of larger soil invertebrates, particularly earthworms. Currently, there is little information available on feeding habits of Mexican and Central American shrews, especially in regions where closely related species are sympatric.

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