

STABLE ISOTOPE RATIOS ($\delta^{15}\text{N}$ AND $\delta^{13}\text{C}$) OF
SYNTOPIC SHREWS (*SOREX*)

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ABSTRACT—Local species richness in shrew (Soricidae) assemblages is often high, and the mechanisms of ecological separation remain relatively unexplored. In this study, hair samples from 6 species of *Sorex* in 3 separate assemblages were analyzed for stable carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) isotope ratios to investigate dietary differences. At each locality, common species exhibited a broad range in $\delta^{15}\text{N}$ and, to a lesser extent, $\delta^{13}\text{C}$, whereas non-overlapping signatures characterized the less abundant species. Because the naturally occurring stable isotope ratios of carbon and nitrogen vary with microenvironment and trophic level, the results support the idea that shrews achieve coexistence through resource partitioning. This study is the first to report stable isotope data on syntopic shrews and provides a direction for future research into resolving the mechanisms of ecological separation in shrew communities.

RESUMEN—La riqueza local de las especies en comunidades de la musaraña (Soricidae) con frecuencia es alta y los mecanismos de separación ecológica siguen siendo relativamente inexplorados. En este estudio, las muestras del pelo de 6 especies de *Sorex* en 3 comunidades separadas fueron analizadas para calcular las proporciones de los isótopos estables de carbón ($^{13}\text{C}/^{12}\text{C}$) y de nitrógeno ($^{15}\text{N}/^{14}\text{N}$) para investigar diferencias dietéticas. En cada lugar, las especies comunes exhibieron una amplia gama en $\delta^{15}\text{N}$, y un poco menos en $\delta^{13}\text{C}$, mientras que proporciones no sobrepuestas caracterizaron las especies menos abundantes. Porque las proporciones de los isótopos estables de carbón y de nitrógeno existen naturalmente, varían con el microambiente y el nivel trófico, los resultados apoyan la idea de que las musarañas alcanzan coexistencia por medio de división de recursos. Este es el primer estudio en divulgar datos de los isótopos estables de musarañas sintópicas, y provee una dirección para la investigación futura para resolver los mecanismos de la separación ecológica en comunidades de musarañas.

Resource partitioning underlies the coexistence of morphologically and ecologically similar species in conditions where resources are limiting (Schoener, 1974a). Among soricine shrews, local species richness is often high (Spencer and Pettus, 1966; Wrigley et al., 1979; Whittaker and French, 1984; Kirkland et al., 1997; Rychlik, 2000). For these small, non-hibernating mammals with high metabolic demands and little gross morphological differentiation, asymmetrical use of prey resources might contribute significantly to ecological separation (Kirkland, 1991). For example, Churchfield (1984) found that the proportions of prey taxa in feces differed among co-occurring shrew species, demonstrating dietary sep-

aration. Other studies suggest a host of mechanisms contributing to ecological separation, including macrohabitat and microhabitat affinities, foraging behavior, body size, vertical stratification, and territoriality (Getz, 1961; Michielsen, 1966; Hawes, 1977; Ellenbroek, 1980; Dickman, 1988; Rychlik, 1997, 2000; Brannon, 2000). Additionally, there are indications that the diets of numerically dominant species of shrews are broad compared with those of less common species (Pernetta, 1976; Whitaker and Maser, 1976). Ultimately, differences in habitat selection could lead to differences in prey encounter rate, hence dietary separation. Our study focused on the distribution patterns of isotopic profiles among syntopic soricids as

an inquiry into the potential utility of stable isotope methods to investigate issues of ecological separation in shrew assemblages.

Analysis of the naturally occurring stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) in animal tissues increasingly is used to provide insights into animal ecology (Gannes et al., 1997). The application of this method potentially is useful for shrew ecology, where direct observation is impractical. Different animal tissues have distinctly different turnover rates (Tieszen et al., 1983; Hobson, 1993); thus, the choice of tissue for isotopic analysis is key. Hair is an extremely useful tissue for examining both modern and historical diets of animals (Schoeninger et al., 1998; O'Connell and Hedges, 1999; Hobson et al., 2000; West et al., 2004). The carbon and nitrogen ratios recorded in the hair reflect the diet at the time of hair growth and remain immobile thereafter (Macko et al., 1999). Thus, hair provides an integrated dietary signal, rather than just an indication of the last meal eaten by the animal, as provided by gut content or fecal analysis.

Isotopic analysis currently cannot provide the resolution to detail taxonomic differences in prey selection. However, it can provide insight into variability of prey selection that enables inferences about trophic level ($^{15}\text{N}/^{14}\text{N}$), food sources for herbivorous prey ($^{13}\text{C}/^{12}\text{C}$), and variation in microhabitat affinities among prey of co-occurring shrews. Differences in the ratios of nitrogen isotopes can be used to infer differences in the trophic levels (Minigawa and Wada, 1984; Schoeninger and DeNiro, 1984). The ratios of carbon isotopes distinguish between plants with the C_3 photosynthetic pathway, typically grasses (averaging -26.5‰), versus plants with the C_4 photosynthetic pathway, mostly dicots (averaging -12.5‰) (Smith, 1972). Terrestrial plants can vary widely in $\delta^{15}\text{N}$ across large spatial scales primarily due to variations in soil $\delta^{15}\text{N}$ (Shearer et al., 1979; Shearer and Kohl, 1989) and the enrichment of deep-rooted plants over those with shallow roots (Virginia et al., 1989). Although communities in this study were sampled over small spatial scales, reducing the potential for appreciable baseline isotopic variation, microenvironmental patchiness in soil properties, climate, moisture, and vegetation structure can influence carbon and nitrogen isotope ratios

of plants and the trophic systems they support (Marriott et al., 1997; Rice, 2000). Thus, many factors determine the isotopic profile of soil epifauna and the shrews that prey on them. The "isotopic niche" of a shrew is therefore defined by both prey affinities and habitat selection. In this way, stable isotopes have been used to infer resource partitioning in aquatic and soil invertebrate communities (Meili et al., 1996; Hendrix et al., 1999; Vaz et al., 1999).

We used the dual isotope ratios of $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ from bulk hair samples of 6 species of shrews (*Sorex cinereus*, *S. monticolus*, *S. nanus*, *S. palustris*, *S. preblei*, and *S. vagrans*) to investigate ecological separation within species assemblages at 3 local sites in Utah. Because shrews sampled in this study were syntopic and trapped synchronously, these assemblages offer an excellent opportunity to investigate niche partitioning.

METHODS—Study Localities and Species—During the summers of 1997 and 1998, 4 species were collected from 2 localities in the La Sal Mountains of southeastern Utah (Appendix I) (Rickart and Heaney, 2001). In the vicinity of Warner Lake, over a period of 11 d, 3 species (*S. cinereus*, $n = 3$; *S. monticolus*, $n = 18$; *S. nanus*, $n = 2$) were collected in a small grove of aspen (*Populus tremuloides*) along the margin of a talus slope (2,850 m elevation), and a fourth species, (*S. palustris*, $n = 2$) was trapped along an adjacent stream. Also in the La Sal Mountains, near the head of Dark Canyon (3,200 m elevation), 3 species (*S. monticolus*, $n = 5$; *S. nanus*, $n = 2$; *S. palustris*, $n = 1$) were collected over a 2-d period at a spring along the margin of a talus field. Specimens from both the Warner Lake and Dark Canyon localities were preserved initially in 10% formalin and subsequently stored in 70% ethyl alcohol for 3.5 to 4.5 y prior to isotopic analysis.

In 2001 and 2002, we collected 2 species in a salt-grass (*Distichlis stricta*) marsh at Timpie Springs Waterfowl Management Area in northwestern Utah (Appendix I). Specimens of *S. vagrans* ($n = 28$) were collected between June 2001 and April 2002, and *S. preblei* ($n = 2$) were collected on 6 March 2002. Specimens from this locality were stored at -20°C for 1 to 8 mo prior to collection of hair samples for isotopic analysis. They subsequently were preserved in 10% formalin and stored in 70% ethyl alcohol. Additional hair samples were collected from 28 specimens from Timpie Springs after 12 mo of fluid preservation. These samples, along with unpreserved hair samples from the same specimens were analyzed concurrently to determine the preservation ef-

fects of formalin and ethanol on stable isotope ratios.

Shrews were identified on the basis of external and cranial measurements and dental characteristics (Junge and Hoffmann, 1981) and retained as voucher specimens (Appendix I). Furthermore, animals collected synchronously were examined for age and molt status.

Sample Preparation and Isotopic Analysis—All specimens were rinsed with 70% ethyl alcohol prior to hair collection. About 1 mg of hair was trimmed from the rump of all specimens and dried in an oven at 55°C for 12 to 24 h. Dried hair was loaded into tin capsules for isotopic analysis (Bol and Pflieger, 2002). Samples were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in a Carlo Erba elemental analyzer (EA 1108) coupled with a Delta-S continuous-flow isotope ratio-mass spectrometer (Finnagen Mat). The standard deviation for replicate measurements of a yeast standard was $<0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Isotope ratios are expressed in ‰ as:

$$\delta^{\text{NE}} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$$

where N is the mass of the heavy isotope of element E and R is the ratio of the heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). The δ values are reported relative to the international standards of Peedee belemnite marine limestone ($\delta^{13}\text{C}$) and atmospheric N_2 ($\delta^{15}\text{N}$).

We calculated 95% confidence intervals of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *S. monticolus* at Warner Lake and represent this region of the unknown mean as an ellipse.

RESULTS—Fluid preservation had a variable but small effect on the isotope ratios of hair samples ($\Delta\delta^{13}\text{C}_{\text{ave}} = -0.44 \pm 0.58\text{‰}$ SD; $\Delta\delta^{15}\text{N}_{\text{ave}} = +0.74 \pm 0.54\text{‰}$ SD). This variation might be the result of a combination of factors, including natural variation in hair samples, formalin-induced fractionation (Sarakinis et al., 2002), residual ethanol, and analytical error. While the source of variation is unclear, the magnitude of change is small; thus, the outcome of this investigation is not appreciably changed. The mean fractionation values above were used to correct signatures from fluid preserved specimens (Warner Lake and Dark Canyon).

On the basis of dental wear and pelage condition, all synchronously trapped animals apparently were young adults and likely were born in the late spring or early summer before collection. We did not encounter specimens that appeared to be old adults that had survived a winter season, nor did we find signs of

molt occurring in any of the shrews. As such, it was assumed that hair isotope values reflect the first adult pelage and likely that of a spring and early summer diet.

We determined stable isotope signatures from 64 specimens representing 6 species of *Sorex*. At each of the 3 localities, the numerically dominant species evinced a broad range in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Fig. 1). Although sample sizes of the less common species were small, these taxa were relatively grouped and seemed to have unique species signatures.

At the Warner Lake locality (Fig. 1a), the distribution of *S. monticolus*, *S. nanus*, and *S. cinereus* values were primarily along the $\delta^{15}\text{N}$ axis, whereas the 2 *S. palustris* specimens were distinguished by their depleted $\delta^{13}\text{C}$ signatures. Similarly, the values for *S. nanus* had a highly enriched $\delta^{15}\text{N}$ range and were separated from all other specimens at this locality. The 3 *S. cinereus* specimens occupied a small range within the range of *S. monticolus*.

Although small sample sizes at Dark Canyon hinder interpretations, the $\delta^{15}\text{N}$ range of *S. monticolus* was large and the depleted $\delta^{13}\text{C}$ signal of the *S. palustris* specimen was noteworthy (Fig. 1b). At Timpie Springs, the ranges in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the March 2002 specimens of *S. vagrans* were large but did not overlap those of the 2 *S. preblei* (Fig. 1c). Furthermore, the *S. preblei* specimens occupied the depleted end of all 28 *S. vagrans* specimens in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at this locality.

DISCUSSION—Overall, our results indicated that co-occurring shrews were partitioning their environment in ways to lead to differences in diet. Although this study represents the most detailed isotopic analysis of these taxa to date, our results did not enable us to determine whether syntopic shrews were specifically exploiting different prey species or preferentially foraging in different microhabitats that hosted the same prey taxa but had different baseline isotope conditions. If, as in the former instance, isotopic differences reflect interspecific dietary differences in shrews, this might result from differences in prey encounter rate (Churchfield, 1994). Invertebrates demonstrate microhabitat affinities (Adis and Ribeiro, 1989; McIntyre, 1998; Powers et al., 1998); thus, even if shrews forage opportunistically, mechanisms such as differences in microhabi-

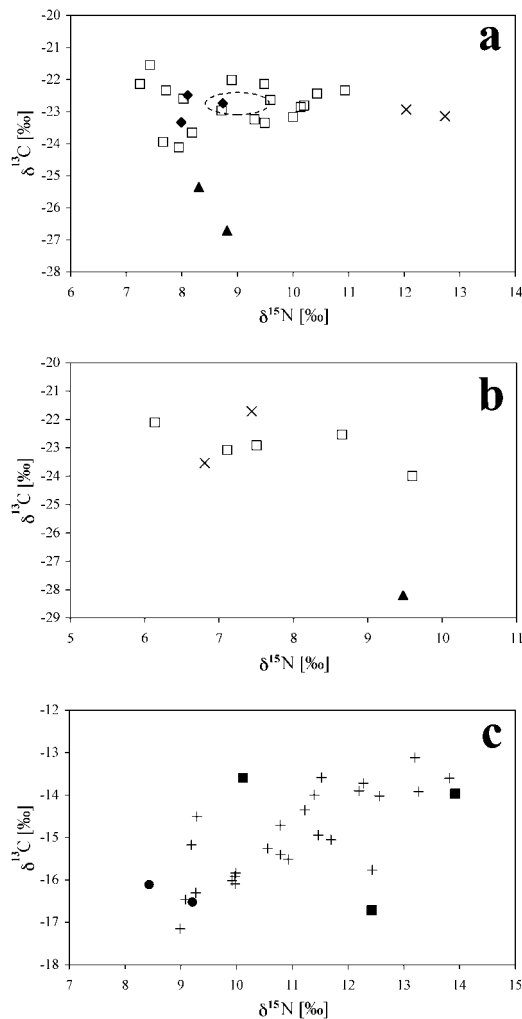


FIG. 1.—Values of $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ from hair samples taken from syntopic and synchronously trapped shrews at 3 locations in Utah: Warner Lake (a), Dark Canyon (b), and Timpie Springs (c). Figure symbols: *Sorex cinereus* (filled diamonds); *S. monticolus* (open squares); *S. palustris* (filled triangles); *S. nanus* (x); *S. preblei* (filled circles); *S. vagrans* (filled squares denote 6 March 2002 collection, and + symbol denotes June 2001 through April 2002 collections, excluding 6 March 2002 specimens). A 95% confidence ellipse is plotted for the *S. monticolus* values from Warner Lake (a). Due to the peripheral distribution of *S. monticolus* values, this region of the unknown mean encompasses only 1 specimen.

tat affinities, vertical stratification, foraging behavior, and body size ultimately might lead to interspecific differences in prey encounter rates, resulting in dietary separation. Other sources of variance in the abundances of ^{15}N include spatial variation in soil nitrogen mineralization and anthropogenic influences, such as land clearing and fertilization (Feigin et al., 1974; Nadelhoffer and Fry, 1994). However, the collection sites in this study represented uncultivated and undisturbed habitat, so anthropogenic influences were minimized, and an understanding of natural isotopic variation in microhabitats, including soil ^{15}N , and potential prey could permit a detailed blueprint of the specific mechanisms employed by shrews faced with competition.

Life stage and nutritional status can influence $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in animal tissue (Hobson et al., 1993; Oelbermann and Scheu, 2002). These effects are minimized because shrews are congeners of similar size and thermoregulatory physiology. And although specimens in this study were potentially nutritionally stressed during capture, bulk hair samples reflect the isotopic composition of the diet during growth, not the last hours of the animal. Nevertheless, because invertebrate prey are subject to these same influences, some of the isotopic variation observed in the shrews might result from affinities among certain species or individuals for different developmental stages of the same invertebrate prey.

The wide range (4‰) in $\delta^{15}\text{N}$ for *S. monticolus* and *S. vagrans* at Warner Lake and Timpie Springs, respectively, could imply that animals were feeding at different trophic levels, because ^{15}N becomes enriched by 3 to 4‰ per trophic level (Minigawa and Wada, 1984; Schoeninger and DeNiro, 1984). However, because dietary overlap in syntopic soricids often is high (Pernetta, 1976; Whitaker and Maser, 1976; Churchfield, 1984; Whitaker and French, 1984), it might be more likely the result of differences in the proportions of certain prey (e.g., predatory versus herbivorous arthropods) that animals were consuming. A generalized diet might help to explain the widespread and abundant distribution of *S. monticolus* (George, 1999).

At Warner Lake the non-overlapping ranges in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *S. monticolus*, *S. nanus*, and *S. palustris* suggest ecological separation among

these species. For *S. nanus*, the enrichment in ^{15}N was perhaps the result of a diet composed primarily of predatory arthropods, such as spiders, a specialization that might result from a microhabitat affinity for rocky areas. It has been suggested that the flattened cranium and small size of *S. nanus* are adaptations for exploiting small prey, such as spiders, insect larvae, and adult small insects often abundant in rocky habitats (Hoffmann, 1999). *Sorex palustris* has morphological adaptations for a semi-aquatic lifestyle (Harris, 1999), which could provide a variety of prey unavailable to terrestrial congeners. The depleted $\delta^{13}\text{C}$ signature for this species at both Warner Lake and Dark Canyon localities indicated that C_3 plants form the trophic base for invertebrate prey. The 2 most similarly sized shrews from Warner Lake, *S. monticolus* and *S. cinereus*, expressed isotopic values indistinguishable from each other and consequently might have significant dietary overlap.

At Timpie Springs, shrews were captured over 11 mo, providing a time dimension not available for the other 2 localities. Of the 5 specimens collected on 6 March 2002, the 2 *S. preblei* were depleted in both ^{15}N and ^{13}C compared to the 3 *S. vagrans* specimens. This general pattern held true with the addition of 25 *S. vagrans* specimens collected over the 11-mo period. Because the 5 specimens from March form the perimeter of isotope values for all 30 specimens from this assemblage, the data suggest that these March values are a reliable estimate of the isotopic variance in this assemblage.

We analyzed shrews that were collected synchronously to control for temporal variation in diet that could result from seasonal changes in prey availability. In a live-trapping study by Churchfield (1984), there were no significant differences in the diversity of prey recorded in fecal samples between summer and winter, but there were differences in the proportions of prey. Sampling in our study coincided with abundant prey seasons, and theory suggests (Schoener, 1974b) that predators should be maximally specialized during abundant seasons. Although sample sizes in this study were small, due to the practical constraints of synchronous collection and the general difficulty of capturing small soricids (Kirkland, 1991; Kirkland and Sheppard, 1994), dietary separation

between species was evident in all 3 assemblages and the strength of this trend was commensurate with sample size.

As a direction for future stable isotope research into the ecological separation of co-occurring soricids, we recommend sampling during seasons of peak and truncated prey abundances to examine how fluctuating resources might influence dietary separation. If the major prey taken by different shrew species is in proportion to their local abundances, dietary overlap and, hence, isotopic overlap should increase during lean seasons. We further suggest comparisons of conspecifics from species assemblages of variable size. If competition influences dietary breadth, the breadth of isotopic range exhibited by a particular species might vary as an inverse function of the number of species in the assemblage.

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LITERATURE CITED

- ADIS, J., AND M. O. D. A. RIBEIRO. 1989. Impact of deforestation on soil invertebrates of floodplain forests in central Amazonia Brazil and their strategies for survival during long periods of flooding. *Boletim do Museu Paraense Emilio Goeldi Serie Zoologia* 5:101–126.
- BOL, R., AND C. PFLIEGER. 2002. Stable isotope (^{13}C , ^{15}N and ^{34}S) analysis of the hair of modern humans and their domestic animals. *Rapid Communications in Mass Spectrometry* 16:2195–2200.
- BRANNON, M. P. 2000. Niche relationships of two syntopic species of shrews, *Sorex fumeus* and *S. cinereus*, in the southern Appalachian Mountains. *Journal of Mammalogy* 81:1053–1061.
- CHURCHFIELD, S. 1984. Dietary separation in three species of shrews inhabiting water-cress beds. *Journal of Zoology, London* 204:211–228.
- CHURCHFIELD, S. 1994. Foraging strategies of shrews, and the evidence from field studies. In: Merritt, J. F., G. L. Kirkland, Jr., and R. K. Rose, editors. *Advances in the biology of shrews*. Special Pub-

- lication of the Carnegie Museum of Natural History, Pittsburgh 18:77–87.
- DICKMAN, C. R. 1988. Body size, prey size, and community structure in insectivorous mammals. *Ecology* 69:569–580.
- ELLENBROEK, F. J. M. 1980. Interspecific competition in the shrews *Sorex araneus* and *Sorex minutus* (Soricidae, Insectivora): a population study of the Irish pygmy shrew. *Journal of Zoology, London* 192:119–136.
- FEIGIN, A., G. SHEARER, D. H. KOHL, AND B. COMMONER. 1974. The amount and nitrogen-15 content of nitrate in soil profiles from two central Illinois fields in a corn-soybean rotation. *Soil Science Society of America Proceedings* 38:465–471.
- GANNES, L. Z., D. M. O'BRIEN, AND C. M. DEL RIO. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* 78:1271–1276.
- GEORGE, S. B. 1999. Montane shrew, *Sorex monticolus*. In: Wilson, D. E., and S. Ruff, editors. The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, D.C. Pp. 31–33.
- GETZ, L. L. 1961. Factors influencing the local distribution of shrews. *American Midland Naturalist* 65:67–88.
- HARRIS, A. H. 1999. Water shrew, *Sorex palustris*. In: Wilson, D. E., and S. Ruff, editors. The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, D.C. Pp. 38–39.
- HAWES, M. L. 1977. Home range, territoriality, and ecological separation in sympatric shrews, *Sorex vagrans* and *Sorex obscurus*. *Journal of Mammalogy* 58:354–367.
- HENDRIX, P. F., S. L. LACHNIGHT, M. A. CALLAHAM, JR., AND X. ZOU. 1999. Stable isotopic studies of earthworm feeding ecology in tropical ecosystems of Puerto Rico. *Rapid Communications in Mass Spectrometry* 13:1295–1299.
- HOBSON, K. A. 1993. Trophic relationships among high arctic seabirds: insights from tissue-dependent stable-isotope models. *Marine Ecology Progress Series* 95:7–18.
- HOBSON, K. A., R. T. ALISAUSKAS, AND R. G. CLARK. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95:388–394.
- HOBSON, K. A., B. N. McLELLAN, AND J. G. WOODS. 2000. Using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology* 78:1332–1339.
- HOFFMANN, R. S. 1999. Dwarf shrew, *Sorex nanus*. In: Wilson, D. E., and S. Ruff, editors. The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, D.C. Pp. 33–34.
- JUNGE, J. A., AND R. S. HOFFMANN. 1981. An annotated key to the long-tailed shrews (genus *Sorex*) of the United States and Canada, with notes on Middle American *Sorex*. *Occasional Papers of the Museum of Natural History, University of Kansas* 94: 1–48.
- KIRKLAND, G. L., JR. 1991. Competition and coexistence in shrews (Insectivora: Soricidae). In: Findley, J. S., and T. L. Yates, editors. The biology of the Soricidae. Special Publication of the Museum of Southwestern Biology, University of New Mexico, Albuquerque. Pp. 15–22.
- KIRKLAND, G. L., JR., R. P. PARMENTER, AND R. E. SKOOG. 1997. A five-species assemblage of shrews from the sagebrush-steppe of Wyoming. *Journal of Mammalogy* 78:83–89.
- KIRKLAND, G. L., JR., AND P. K. SHEPPARD. 1994. Proposed standard protocol for sampling small mammal communities. In: Merritt, J. F., G. L. Kirkland, Jr., and R. K. Rose, editors. Advances in the biology of shrews. Special Publication of Carnegie Museum of Natural History, Pittsburgh 18:277–281.
- MACKO, S. A., M. H. ENGEL, V. ANDRUSEVICH, G. LUBEC, T. C. O'CONNELL, AND R. E. M. HEDGES. 1999. Documenting the diet in ancient human populations through stable isotope analysis of hair. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 354:65–76.
- MARRIOTT, C. A., G. HUDSON, D. HAMILTON, R. NEILSON, B. BOAG, L. L. HANDLEY, J. WISHART, C. M. SCRIMGEOUR, AND D. ROBINSON. 1997. Spatial variability of soil total C and N and their stable isotopes in an upland Scottish grassland. *Plant and Soil* 196:151–162.
- MCINTYRE, N. E. 1998. Abundance and habitat affinities of *Cyclotrachelus substriatus* (Coleoptera: Carabidae) on northern shortgrass prairie. *Prairie Naturalist* 30:157–168.
- MEILI, M., G. W. KLING, B. FRY, R. T. BELL, AND I. AHLGREN. 1996. Sources and partitioning of organic matter in a pelagic microbial food web inferred from the isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of zooplankton species. *Ergebnisse-der-Limnologie* 48:53–61.
- MICHELSEN, C. N. 1966. Intraspecific and interspecific competition in the shrews *Sorex araneus* and *Sorex minutus* L. *Archives Neerlandaises de Zoologie* 17:73–174.
- MINIGAWA, M., AND E. WADA. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relationship between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 50:2143–2146.
- NADELHOFFER, K. J., AND B. FRY. 1994. Nitrogen iso-

- tope studies in forest ecosystems. In: Lajtha, K., and R. H. Michener, editors. *Stable isotopes in ecology and environmental science*. Blackwell Scientific, Oxford, United Kingdom. Pp. 22–44.
- O'CONNELL, T. C., AND R. E. M. HEDGES. 1999. Investigations into the effect of diet on modern human hair isotopic values. *American Journal of Physical Anthropology* 108:409–425.
- OELBERMANN, K., AND S. SCHEU. 2002. Stable isotope enrichment ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): effects of prey quality. *Oecologia* 130:337–344.
- PERNETTA, J. C. 1976. Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grassland. *Journal of Animal Ecology* 45:899–912.
- POWERS, L. E., M. HO, D. W. FRECKMAN, AND R. A. VIRGINIA. 1998. Distribution, community structure, and microhabitats of soil invertebrates along an elevational gradient in Taylor Valley, Antarctica. *Arctic and Alpine Research* 30:133–141.
- RICE, S. K. 2000. Variation in carbon isotope discrimination within and among *Sphagnum* species in a temperate wetland. *Oecologia* 123:1–8.
- RICKART, E. A., AND L. R. HEANEY. 2001. Shrews of the La Sal Mountains, southeastern Utah. *Western North American Naturalist* 61:103–108.
- RYCHLIK, L. 1997. Differences in foraging behaviour between water shrews: *Neomys anomalus* and *Neomys fodiens*. *Acta Theriologica* 42:351–386.
- RYCHLIK, L. 2000. Habitat preferences of four sympatric species of shrews. *Acta Theriologica* 45:173–190.
- SARAKINOS, H. C., M. L. JOHNSON, AND M. J. VANDER ZANDEN. 2002. A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. *Canadian Journal of Zoology* 80:381–387.
- SCHOENER, T. W. 1974a. Resource partitioning in ecological communities. *Science* 185:27–39.
- SCHOENER, T. W. 1974b. The compression hypothesis and temporal resource partitioning. *Proceedings of the National Academy of Science* 71:4169–4172.
- SCHOENINGER, M. J., AND M. J. DENIRO. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta* 48:625–639.
- SCHOENINGER, M. J., U. T. IWANIEC, AND L. T. NASH. 1998. Ecological attributes recorded in stable isotope ratios of arboreal primate hair. *Oecologia* (Berlin) 113:222–230.
- SHEARER, G. B., D. H. KOHL, AND S. H. CHIEN. 1979. The nitrogen-15 abundance in a wide variety of soils. *Soil Science Society of America Journal* 42:899–902.
- SHEARER, G., AND D. H. KOHL. 1989. Estimates of N_2 fixation in ecosystems: the need for and basis of the ^{15}N natural abundance method. In: Rundel, P. W., J. R. Ehleringer, and K. A. Nagy, editors. *Stable isotopes in ecological research*. Springer-Verlag, New York. Pp. 342–347.
- SMITH, B. N. 1972. Natural abundance of the stable isotopes of carbon in biological systems. *BioScience* 22:226–231.
- SPENCER, A. W., AND D. PETTUS. 1966. Habitat preferences of five sympatric species of long-tailed shrews. *Ecology* 47:677–683.
- TIESZEN, L. L., T. W. BOUTTON, K. G. TESDAHL, AND N. A. SLADE. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for delta carbon-13 analyses of diet. *Oecologia* (Berlin) 57:32–37.
- VAZ, M. M., M. PETRERE, JR., L. A. MARTINELLI, AND A. A. MOZETO. 1999. The dietary regime of detritivorous fish from the River Jacare Pepira, Brazil. *Fisheries Management and Ecology* 6:121–132.
- VIRGINIA, R. A., W. M. JARRELL, P. W. RUNDEL, G. SHEARER, AND D. H. KOHL. 1989. The use of variation in the natural abundance of ^{15}N to assess symbiotic nitrogen fixation by woody plants. In: Rundel, P. W., J. R. Ehleringer, and K. A. Nagy, editors. *Stable isotopes in ecological research*. Springer-Verlag, New York. Pp. 345–394.
- WEST, A. G., L. K. AYLIFFE, T. E. CERLING, T. ROBINSON, B. KARREN, M. D. DEARING, AND J. EHLERINGER. 2004. Short-term diet changes revealed using stable carbon isotopes in horse tail-hair. *Functional Ecology* 18:616–624.
- WHITAKER, J. O., JR., AND T. W. FRENCH. 1984. Foods of six species of sympatric shrews from New Brunswick. *Canadian Journal of Zoology* 62:622–626.
- WHITAKER, J. O., JR., AND C. MASER. 1976. Food habits of five western Oregon shrews. *Northwest Science* 50:102–107.
- WRIGLEY, R. E., J. E. DUBOIS, AND H. W. R. COPLAND. 1979. Habitat, abundance, and distribution of six species of shrews in Manitoba. *Journal of Mammalogy* 60:505–520.

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APPENDIX I—*Specimens Examined*—The following 64 specimens examined for stable isotope signatures are housed at the Field Museum (FMNH) and the Utah Museum of Natural History (UMNH).

Sorex cinereus ($n = 3$): Utah, Grand County, La Sal Mountains, 0.7 km N, 0.4 km W Warner Lake, 38°31'30"N, 109°16'40"W, 2,850 m elevation (FMNH 162898; UMNH 29935, 29936).

Sorex monticolus ($n = 23$): Utah, Grand County, La Sal Mountains, 0.7 km N, 0.4 km W Warner Lake, 38°31'30"N, 109°16'40"W, 2,850 m elevation (FMNH

162899–162905; UMNH 29948–29951, 29953, 29956, 29957, 29959–29962); San Juan County, La Sal Mountains, head of Dark Canyon, N base of Mount Peale, 38°27'N, 109°13'15"W, 3,200 m elevation (UMNH 29809, 29815–29818).

Sorex nanus ($n = 4$): Utah, Grand County, La Sal Mountains, 0.7 km N, 0.4 km W Warner Lake, 38°31'30"N, 109°16'40"W, 2,850 m elevation (FMNH 162958, 162959); San Juan County, La Sal Mountains, head of Dark Canyon, N base of Mount Peale, 38°27'N, 109°13'15"W, 3,200 m elevation (UMNH 29808, 29810).

Sorex palustris ($n = 4$): Utah, Grand County, La Sal Mountains, 0.7 km N, 0.4 km W Warner Lake, 38°31'30"N, 109°16'40"W, 2,850 m elevation (UMNH 29999, 30007, 30009); San Juan County, La Sal Mountains, head of Dark Canyon, N base of Mount Peale, 38°27'N, 109°13'15"W, 3,200 m elevation (UMNH 29819).

Sorex preblei ($n = 2$): Utah, Tooele County, Timpie Springs Waterfowl Management Area, 40°45'N, 112°38'W, 1,285 m elevation (UMNH 30396, 30397).

Sorex vagrans ($n = 28$): Utah, Tooele County, Timpie Springs Waterfowl Management Area, 40°45'N, 112°38'W, 1,285 m elevation (UMNH 30400–30427).