



Niche differentiation among small mammals of the Alexander Archipelago in southeastern Alaska

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We compared isotopic niche widths of small mammals that co-occur across the Alexander Archipelago and adjacent mainland in southeastern Alaska to test the prediction that dietary niche widths will be greater for individuals living in communities with fewer potential competitors and predators. We quantified the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic niche widths of 2 insectivorous shrews (*Sorex cinereus* and *S. monticola*), 3 primarily herbivorous rodents (*Microtus longicaudus*, *M. oeconomus*, and *M. pennsylvanicus*), and 1 omnivorous rodent (*Peromyscus keeni*) and combined these data with information provided by natural history accounts. We sampled islands that varied with respect to size and species richness to compare with localities on the adjacent mainland, where species richness is greatest. Consistent with our predictions, isotopic niche widths were significantly greater on islands relative to mainland localities. Our findings can help guide management strategies within this archipelago through increased understanding of how key community-level interactions vary across localities within this complex landscape.

Key words: community dynamics, islands, species interactions, stable isotopes

Understanding the factors that influence niche width is crucial to determining how environmental change may impact community-level interactions, which are critical components of forecasting the long-term persistence of species and ensuring their effective management and conservation. Populations isolated on islands distributed across archipelagos provide natural experimental replicates to test fundamental niche concepts (Santos et al. 2016), such as the relationship between island size and foraging niche width (e.g., Scott et al. 2003; Darimont et al. 2009), the role of competition among closely related species with similar diets (e.g., Robinson-Wolrath and Owens 2003; Buckley and Roughgarden 2006), and the role predation plays in the foraging decisions and realized niches of prey species (e.g., Lomolino 1984; Fey et al. 2008).

Traditionally, niche width has been assessed through direct observation or by analysis of scat or stomach contents (e.g., Van Valen 1965; Roughgarden 1972; Masson 1975; Lister 1976). Not only are these traditional methods time-consuming and difficult to employ for multiple species over large regions, but such

measures only provide information about resources consumed in the past ~24–48 h (Bearhop et al. 2004) and thus may not accurately represent the typical diet of a species. Stable isotope analysis provides an alternative method to traditional proxies, which is especially useful for assessing trophic niche width (Bearhop et al. 2004; Newsome et al. 2007; Bond et al. 2016). The isotopic composition of animal tissues mirrors that of their food but is offset in a predictable manner due to physiological processes that sort isotopes during assimilation and excretion (Bearhop et al. 2004; Newsome et al. 2007). Furthermore, the temporal scale over which dietary inputs are integrated varies by tissue type (Martinez del Rio et al. 2009a). For example, isotopic incorporation rates for bone collagen are relatively slow in comparison to other tissues such that collagen integrates multiple years of ecological information (Bearhop et al. 2004). Thus, for short-lived species like most small mammals (Levine 1997), bone collagen carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values can be used to estimate dietary niche width over the majority of an individual's lifetime (Bearhop et al. 2004).

To assess the role that competition and predation play in structuring small mammal communities, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values from bone collagen to quantify intra- and interspecific variation in dietary niches for 6 species of small mammals (*Sorex cinereus*, *S. monticola*, *Microtus longicaudus*, *M. oeconomus*, *M. pennsylvanicus*, and *Peromyscus keeni*) that commonly occur across the Alexander Archipelago. The Alexander Archipelago consists of over 1,000 named islands that vary in size, distance to the mainland, glaciation history, and mammalian species richness (Conroy et al. 1999; Cook et al. 2006; Carrara et al. 2007), with larger islands (> 6,400 km²) generally supporting more diverse mammalian communities than smaller islands (MacDonald and Cook 2007, 2009; Cook and MacDonald 2013). During the Last Glacial Maximum (18 ka), the Cordilleran ice sheet covered most of southeastern Alaska, eliminating habitat for many terrestrial species except for those that persisted in glacial refugia along the outer coast (Carrara et al. 2007; Sawyer and Cook 2016). As ice retreated eastward, newly deglaciated land provided a clean slate for recolonizing species, which arrived from multiple independent refugia as opportunities arose during cyclical glacial retractions (MacDonald and Cook 2007; Cook and MacDonald 2013). This complex biogeographic history (e.g., Hope et al. 2016; Sawyer and Cook 2016) provides an excellent opportunity to explore patterns in small mammal foraging niche width across multiple localities that vary in size and species richness.

Islands, especially small islands, generally have lower species richness relative to adjacent mainland areas (MacArthur et al. 1972). Accordingly, insular species are expected to expand their niche width due to competitive release (Grant 1972). Therefore, we predict that insular populations in the Alexander Archipelago will have broader isotopic niche widths indicative of a more diverse foraging niche in comparison to mainland populations of conspecifics, where we predict that sympatric species will partition or narrow their niches to reduce competition for shared resources (Hardin 1960). Additionally, the risk of predation may impact habitat choices for prey species through nonconsumptive effects (Lima and Dill 1990; Lima 1998; Peckarsky et al. 2008) such that prey undergo spatial shifts, potentially to areas with lower quality or fewer resources in an effort to avoid predation (Barbehenn 1958; Fulk 1972; Carpenter et al. 1987). Thus, we predict that species will have broader isotopic niches at island localities with lower predation risk compared to mainland localities. Our analyses reveal considerable variation in the dietary niche widths of the study species and generate new insights into the potential role of competition and predation in structuring dietary niches across this complex archipelago.

MATERIALS AND METHODS

Study region and species.—We sampled small mammals from 10 islands in the Alexander Archipelago (Admiralty, Annette, Baranof, Chichagof, Kuiu, Kupreanof, Mitkof, Prince of Wales, Revillagigedo, Wrangell) that varied in size and distance to

mainland. We also sampled 3 mainland localities: Excursion Inlet, 2 sites 25 km northeast and northwest of Juneau (considered 1 locality for analysis), and 1 site at Unuk River (Fig. 1; Supplementary Data SD1). All sampling was conducted in or at the edge of old growth forest stands with dominant tree species including Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Alaska yellow cedar (*Cupressus nootkatensis*), and a varied understory of shrubs, herbs, ferns, mosses, and fungi. Our study focused on 6 small mammal species that occupy a variety of dietary niches: cinereus shrews (*Sorex cinereus*), montane shrews (*Sorex monticola*), northwestern deer mice (*Peromyscus keeni*), long-tailed voles (*Microtus longicaudus*), root voles (*Microtus oeconomus*), and meadow voles (*Microtus pennsylvanicus*). Shrews are insectivores (Churchfield 1994; Smith and Belk 1996; Whitaker 2004), voles are primarily herbivores (Reich 1981; Smolen and Keller 1987; Mustonen et al. 2008), and deer mice are omnivores that consume a wide variety of plant and animal matter depending on local availability (Whitaker 1966).

Museum specimen collection.—We used the online museum database ARCTOS (Arctos 2015) to identify existing specimens for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analysis (Supplementary Data SD2). A search for specimens from the 10 islands and 3 mainland localities targeted in this study revealed 340 individuals of the taxa selected for analysis. At 11 of the 13 localities considered, numerous specimens had been collected during the summer (June–August) months. At the remaining sites (Chichagof and Juneau), few specimens had been collected during the summer, so we expanded our database search to include multiple seasons, which were pooled for subsequent analyses. Postcranial bones (vertebrae and ribs) were sampled from skeletons curated at the Museum of Southwestern Biology (MSB) in Albuquerque, New Mexico and the University of Alaska Museum of the North (UAM) in Fairbanks, Alaska.

Stable isotope analysis.—Bone elements were demineralized in 0.5N hydrochloric acid for ~24 h at 5°C. Samples were rinsed to neutrality with deionized (DI) water and collagen was lipid-extracted by immersion in a 2:1 chloroform:methanol solution for ~72 h; the solvent solution was discarded and refreshed with a new aliquot every ~24 h. Samples were then rinsed repeatedly with DI water to remove solvents, after which they were freeze-dried. Approximately 0.5–0.6 mg of dried collagen was weighed into 3 × 5 mm tin capsules and carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values were measured on a Costech 4010 elemental analyzer (Costech Analytical Tech Inc., Valencia, California) coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., Santa Fe, New Mexico) at the University of New Mexico Center for Stable Isotopes (Albuquerque, New Mexico). Stable isotope data are expressed as δ values, $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1,000 * [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}]$, where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ of the sample and standard, respectively. The internationally accepted standards for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are Vienna Pee Dee Belemnite (V-PDB) and atmospheric

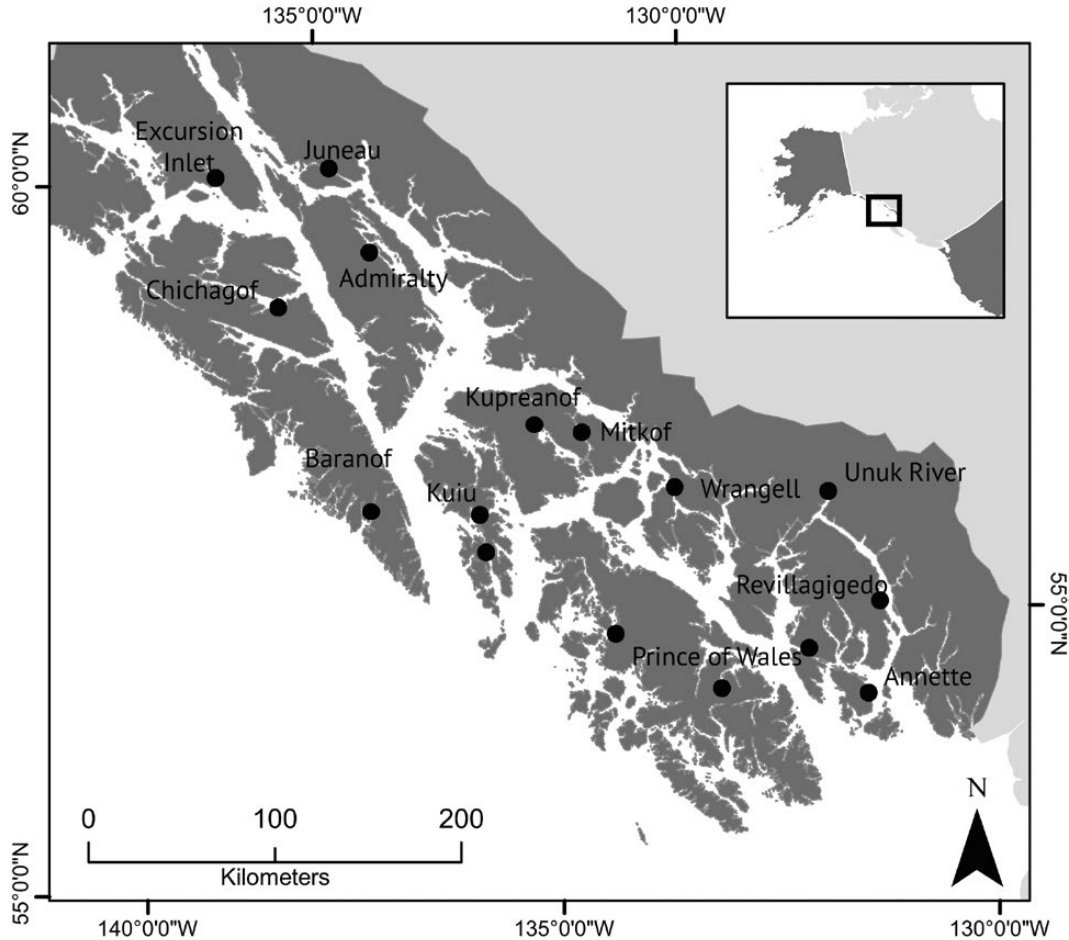


Fig. 1.—Map of the Alexander Archipelago of southeastern Alaska showing localities where small mammal specimens were collected. Black box denotes location of Alexander Archipelago in relation to mainland Alaska.

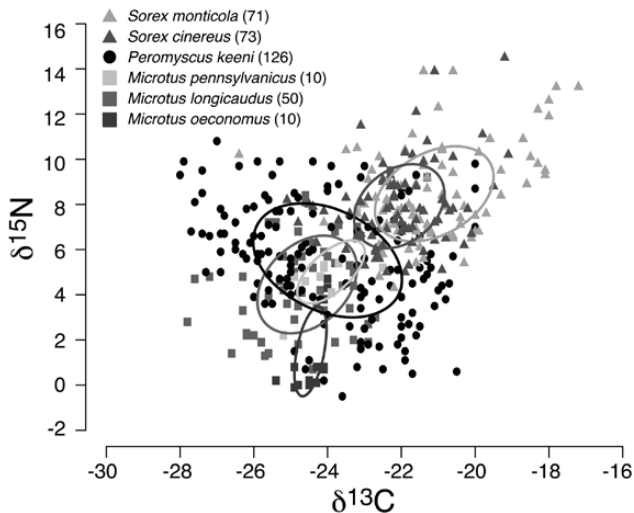


Fig. 2.— $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ isotopic niche space (SEA_B or SEA_C in ‰^2) for all species across all localities in the Alexander Archipelago and adjacent Alaskan mainland; sample sizes are shown in parentheses. SEA = standard ellipse areas.

N_2 respectively, with the units for both expressed as parts per thousand or per mil (‰). Precision was determined by analysis of internal reference materials calibrated to internationally

accepted standards; within-run variation (SD) was $\leq 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. We also measured the weight percent carbon and nitrogen concentrations ($[\text{C}]/[\text{N}]$) of each sample; all samples had $[\text{C}]/[\text{N}]$ that were similar to the theoretical ratio for bone collagen (Ambrose and Norr 1992).

Statistical analysis.—Statistical analyses were conducted using the package Stable Isotope Analysis in R “siar” (SIAR, Parnell and Jackson 2013) contained in R (R Development Core Team 2013). SIAR contains a supplementary package, Stable Isotope Bayesian Ellipses in R (SIBER), which calculates standard ellipse areas (SEA) in a Bayesian framework (SEA_B in ‰^2) and provides a robust estimate of isotopic niche width for sample sizes ≥ 10 (Jackson et al. 2011); for sample sizes < 10 , we used ellipse estimates corrected for small sample sizes (SEA_C). All specimens of a given species sampled from a given locality were pooled for subsequent analyses. We used SIBER to generate SEA plots with data from all species across all localities (Fig. 2), as well as at each individual locality (Fig. 3).

We calculated SEA for each species at each locality (Table 1) and used these results to determine if dietary niche widths differed with island size. Data on island size were obtained from Cook and MacDonald (2013); mainland localities were given a constant value of $6,000 \text{ km}^2$. We calculated the amount of SEA overlap (‰^2) between isotopic niche widths of co-occurring

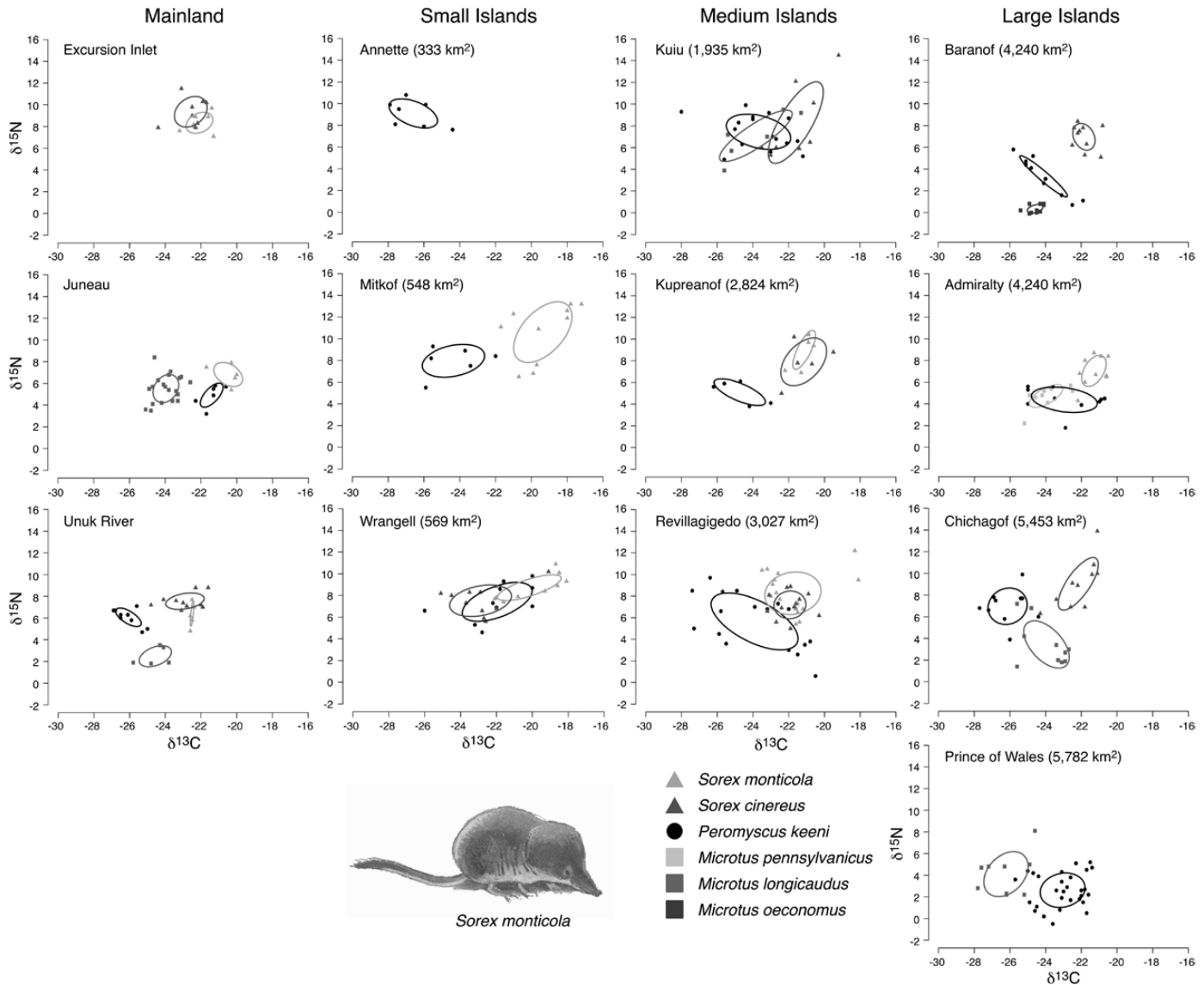


Fig. 3.— $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ isotopic niche space (SEA_B or SEA_C in $\%o^2$) for species by locality in the Alexander Archipelago and adjacent Alaskan mainland. Panels are sorted left to right by island size with mainland localities on the far left. SEA = standard ellipse areas.

species collected from the same locality to indicate the degree that co-occurring species consume similar resources (Fig. 4). We used MacDonald and Cook (2009) to determine the number of small mammal competitor species and the number of mammalian predators present at each locality. We labeled all species within the order Carnivora as potential predators of our focal species (Supplementary Data SD4). We assumed avian predators to have an equal impact on the foraging behavior of the study species at all localities (K. Winker, University of Alaska Museum, Curator of Birds, Fairbanks, Alaska, pers. comm., October 2016) and thus we did not include avian predators in our analyses. We classified small mammal species at a given locality as potential competitors to our focal study species using dietary information provided by individual species accounts (Supplementary Data SD3). We labeled a species as a competitor if their primary diet (herbivore, insectivore, omnivore) overlapped with the primary diet of the species within our study. This assessment did not serve to identify all potential

competitors of our study species but rather was intended to serve as an estimate of the relative degree of competition experienced by conspecifics within island and mainland communities. Variation partitioning was performed in R (R Development Core Team 2013) using the package “vegan” (Oksanen et al. 2017) to disentangle the effects of locality size, distance from mainland, competition, and predation on SEA.

RESULTS

Island size.—For islands with multiple localities sampled (Kuiu, Revillagigedo, and Prince of Wales), 2-sample *t*-tests revealed no significant within-island differences in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values (all $P > 0.05$). Specimens from 4 localities (Chichagof, Juneau, Kuiu, and Revillagigedo) were collected over multiple time periods. Two-sample *t*-tests revealed no significant temporal differences among isotopic values at Kuiu or Revillagigedo (both $P > 0.05$), both of which had been sampled

Table 1.—Mean $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ standard ellipse area (SEA_B in $\%e^2$) and associated error (SD) of each species across each locality in the Alexander Archipelago and adjacent Alaskan mainland. Numbers in parentheses indicate sample size. A corrected SEA (SEA_C) estimate was used for sample sizes less than 10.

Island	Size (km ²)	<i>Microtus longicaudus</i>	<i>Microtus oeconomus</i>	<i>Microtus pennsylvanicus</i>	<i>Peromyscus keeni</i>	<i>Sorex monticola</i>	<i>Sorex cinereus</i>
Annette	333	a	b	b	(7) 4.9 ± 1.9	a	b
Mitkof	548	a	b	a	(6) 7.9 ± 3.1	(10) 10.8 ± 3.6	a
Wrangell	569	a	b	a	(10) 8.1 ± 2.7	(10) 4.7 ± 1.6	(10) 6.8 ± 2.3
Kuiu	1,935	(6) 8.0 ± 3.5	b	b	(16) 8.0 ± 2.1	a	(8) 12.1 ± 4.2
Kupreanof	2,824	a	b	b	(5) 3.8 ± 2.1	(6) 2.3 ± 1.7	(5) 7.9 ± 3.4
Revillagigedo	3,027	a	b	b	(17) 14.8 ± 3.7	(17) 9.0 ± 2.3	(12) 3.6 ± 1.1
Baranof	4,240	b	(10) 1.1 ± 0.4	b	(10) 3.7 ± 1.2	b	(10) 2.7 ± 0.9
Admiralty	4,313	a	b	(10) 2.8 ± 0.9	(10) 5.9 ± 2.0	(10) 3.2 ± 1.1	b
Chichagof	5,453	(10) 6.8 ± 2.2	a	b	(10) 5.4 ± 1.8	b	(10) 6.0 ± 2.0
Prince of Wales	5,782	(9) 7.6 ± 2.5	b	b	(20) 6.0 ± 1.1	a	b
Mainland							
Excursion Inlet		a	a	a	a	(7) 2.7 ± 1.1	(8) 3.9 ± 1.5
Juneau		(20) 3.0 ± 0.7	a	a	(6) 1.7 ± 1.2	(5) 2.6 ± 1.5	a
Unuk River		(5) 2.5 ± 1.5	a	a	(9) 1.4 ± 0.7	(6) 0.3 ± 1.0	(10) 2.7 ± 0.9

^aSpecies occur at locality but were not included due to limited specimen availability.

^bSpecies do not occur at locality.

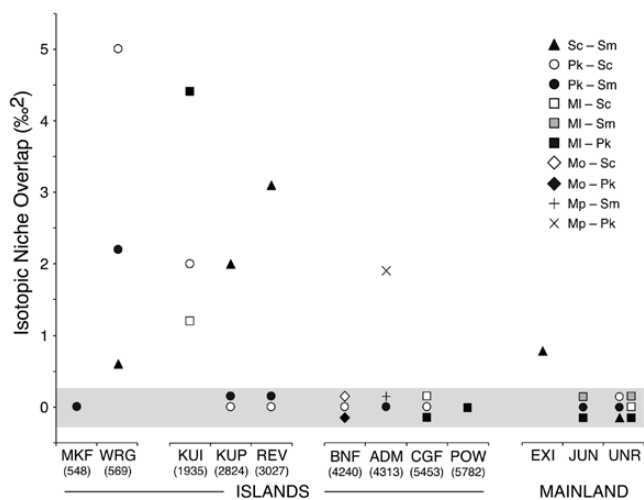


Fig. 4.—Isotopic niche overlap between species by locality in the Alexander Archipelago and adjacent Alaskan mainland; data points within gray bar indicate no overlap. MKF = Mitkof; WRG = Wrangell; KUI = Kuiu; KUP = Kupreanof; REV = Revillagigedo; BNF = Baranof; ADM = Admiralty; CGF = Chichagof; POW = Prince of Wales; EXI = Excursion Inlet; JUN = Juneau; UNR = Unuk River. Annette was excluded because only 1 species (*Peromyscus keeni*) was sampled from this locality. Species acronyms are Sc = *Sorex cinereus*; Sm = *Sorex monticola*; Pk = *Peromyscus keeni*; MI = *Microtus longicaudus*; Mo = *Microtus oeconomus*; Mp = *Microtus pennsylvanicus*. Island size (km²) is reported in parentheses below island name.

during the summer only. In contrast, significant temporal differences in isotope values ($P < 0.001$) were detected for specimens from Chichagof and Juneau. This outcome may reflect the small number of specimens available within each trapping season; as such, results from these 2 localities should be interpreted with caution. Moreover, because isotopic incorporation rates for bone collagen are slow and integrate multiple years of ecological information, these apparent differences may be

due to individual resource specialization as opposed to trapping season. Future collection efforts will focus on increasing specimens from these localities to parse out these effects. When data from all species were combined, there was a significant relationship between locality size and SEA ($F = 17.85_{33}$, $R^2 = -0.33$, $P = 0.0001$). However, this effect seems to be driven by decreased SEA at mainland localities. We used a multiple regression model with mainland as a variable and controlled for differences in apparent level of competition and predation across localities, which revealed that mainland localities had significantly smaller SEA relative to islands ($t = -2.56$, $P = 0.01$). The overall mean ($\pm SD$) SEA for island localities ($X = 6.3 \pm 3.2\%e^2$) was greater than that for mainland localities ($\bar{X} = 2.3 \pm 1\%e^2$). The relationship between SEA , number of competitors or predators, and locality size is illustrated in Supplementary Data SD5.

Competition.—Interspecific differences in $\delta^{15}\text{N}$ values appeared to be associated with assigned trophic categories (insectivore, herbivore, and omnivore) derived from species accounts and field-based observations. When data from all localities were combined, the 2 insectivorous shrew species had the highest $\delta^{15}\text{N}$ values, the omnivorous deer mice had intermediate $\delta^{15}\text{N}$ values, and the 3 herbivorous vole species had the lowest $\delta^{15}\text{N}$ values (Fig. 2). Intraspecific differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied greatly across localities (Fig. 3).

Mainland localities had the greatest number of mammalian species, and therefore the highest potential for competition among small mammals; on islands there were ~25–50% fewer competitor species than on the mainland. We found a significant relationship between SEA and the number of potential competitors when data from all species were combined ($F = 6.12_{33}$, $R^2 = -0.13$, $P = 0.01$).

SEA overlap occurred most frequently at Wrangell and Kuiu, with 3 distinct pairs of overlapping species at each of these sites (Fig. 4); 4 other localities (Kupreanof, Revillagigedo,

Admiralty, and Excursion Inlet) had a single pair of species with overlapping SEA. No overlap of SEA was detected at the remaining 7 localities (Annette, Mitkof, Baranof, Chichagof, Prince of Wales, Juneau, and Unuk River).

Predation.—The mainland localities also had a greater number of species of potential mammalian predators relative to the islands. When all species were considered together, we found a significant relationship between number of potential mammalian predators and SEA ($F = 6.91_{33}$, $R^2 = -0.15$, $P = 0.01$).

Consistent with the relationships suggested by the separate linear regressions, variation partition analysis suggests that locality size (adjusted $R^2 = 0.17$) is the best predictor of isotopic niche width, followed by predation (adjusted $R^2 = 0.12$), with competition (adjusted $R^2 = 0.004$) and distance from mainland (adjusted $R^2 = 0.004$) having a similar effect ($P = 0.01$).

DISCUSSION

Dietary niche widths, as revealed by variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were larger at island localities than the mainland. However, SEA did not seem to vary in a predictable manner based on size (km^2) of individual islands, suggesting that competition or predation may play a larger role in determining the niche width of focal species. Future research will focus on increasing the number of islands sampled in order to gain further insight into the effect of island size on isotopic niche width.

Grant (1972) suggested that niches will expand when species have less competition for resources. Consistent with the theory of competitive release, our results indicate that species have larger SEA on islands, which support fewer competitor species relative to adjacent mainland localities. SEA overlap (an indicator that species are consuming similar resources) occurred most frequently on Wrangell and Kuiu islands—each with 3 distinct occurrences of SEA overlap between species. Wrangell has the highest number of small mammal species ($n = 12$) of all the islands in our study; it is likely that greater species richness and associated competition for resources contributed to the high level of SEA overlap observed on this relatively small island (569 km^2) that is close to the mainland. The mechanism leading to greater SEA overlap on Kuiu is less clear, as this island supports fewer small mammal species ($n = 6$) than other islands of comparable size. Additionally, individuals at this locality maintain similar body mass compared to conspecifics on other medium-sized islands, indicating that differential body mass was not a driver of the observed pattern. The observed SEA overlap between species may be due to a lack of resources on Kuiu, although a systematic measure of consumable resources across localities is necessary to evaluate this hypothesis. Interestingly, Kuiu was the only locality in which *Microtus* and *Sorex* species had overlapping SEA. The comparatively large SEA for *M. longicaudus* on Kuiu (8.0 ‰) likely drives this pattern and suggests that *M. longicaudus* could be omnivorous at this locality.

Kupreanof, Revillagigedo, Admiralty, and Excursion Inlet each had a single occurrence of SEA overlap, whereas species sampled at the remaining localities maintained distinct isotopic

niches with no overlap. These results do not necessarily indicate a lack of competition at these localities, but rather that species sampled at these localities apparently did not consume similar resources and thus maintained distinct SEAs. The focal species may be competing with other species not sampled for this study. Mainland sites had the least amount of SEA overlap among species, both in terms of occurrence as well as degree of overlap. At mainland localities, SEA overlap was found only between closely related species of *Sorex* at Excursion Inlet (Fig. 4) and the degree of overlap was small (0.8 ‰) compared to the average observed overlap between species of *Sorex* at island sites (1.9 ‰). Heightened interspecific competition at mainland localities is likely an important driver leading species to specialize on particular resources (Roughgarden 1974; Bolnick et al. 2003; Araújo et al. 2011).

SEA overlap occurred between 10 different pairs of species among our study sites. Of these, 7 included at least 1 species of *Sorex*, while the remaining 3 pairs included a species of *Microtus* and *P. keeni*. SEA overlap between the 2 species of *Sorex* increased with increased island size, suggesting that increased area alone does not always result in reduced competition. The frequent SEA overlap observed with *Sorex* may be due to the heightened metabolism and elevated energetic demands typical of shrews (Hamilton 1930; Genoud 1985; Ochocińska and Taylor 2005). The average basal metabolic rate of *Sorex* is $\sim 300\%$ higher than that of other mammals of the same body mass (Taylor 1998). Furthermore, lab experiments have shown that in the presence of a perceived (inanimate) competitor, energetic demands of shrews increased significantly (Barnard et al. 1983), indicating that competition may lead shrews to expand their dietary niche to increase their energetic intake and consequently enhance SEA overlap with other species.

The lower amount of SEA overlap among voles and deer mice may be due to the foraging behavior of these species. Food resources required by herbivores (voles) and omnivores (deer mice) are arguably more readily available and easily procured than food resources required by insectivorous shrews, which may allow these species to maintain a lower degree of SEA overlap. Intraspecific competition within generalist species such as *P. keeni* is predicted to increase individual diet specialization, which in turn results in larger population niche widths (Bolnick et al. 2003; Araújo et al. 2011). For example, deer mice on Revillagigedo had the largest SEA (14.8 ‰) recorded for any species in our study, which may be driven by individual diet specialization. Future research utilizing tissues with different isotopic incorporation rates (e.g., liver, muscle, hair) could be combined with the bone collagen data presented here to quantify individual diet specialization in *P. keeni* and other generalist species across the Alexander Archipelago (Martinez del Rio et al. 2009b; Bond et al. 2016). Additionally, the large dietary niche of deer mice likely heightens competitive stress for species like shrews, which have more restricted (specialized) diets, especially on small islands with potentially more limited resource availability. For example, SEA overlap between *P. keeni* and *Sorex* was greatest on the small island, Wrangell, and then decreased with increased island size.

Our analyses suggest that in addition to island size and competition, predation pressure also may influence SEA. Early research argued that predation serves to ease competitive pressure through the reduction (i.e., via consumption) of competing prey species (Paine 1966; Holt 1977). However, recent work shows that species face varying levels of predation risk (Lima 2002) and are thus differentially impacted by the interaction between predation and competition (Hanski and Henttonen 1996). *Sorex monticola*, for example, typically inhabit areas with plentiful herbaceous ground cover that provides some protection against predators (Doyle 1990; Smith and Belk 1996), whereas *S. cinereus* are found in a wider array of habitats such as grasslands, woodlands, and open bogs, which likely results in differential predation risk across species and localities (Whitaker 2004). As exemplified by the frequent SEA overlap between species of *Sorex*, competitive pressure is not entirely eased by predation. In fact, predation risk may heighten competitive stress by driving prey species to occupy a narrower range of habitats and limiting access to otherwise consumable resources (Barbehenn 1958; Fulk 1972; Carpenter et al. 1987; Lima and Dill 1990; Lima 1998; Peckarsky et al. 2008). SEAs at our localities decreased as the level of apparent predation increased. Research in both field and laboratory settings has shown an effect of predation risk on the foraging behavior of a variety of species, including gerbils (Kotler et al. 1991), marmots (Holmes 1984), voles (Taitt et al. 1981), desert rodents (Kotler 1984), ungulates (Hebblewhite et al. 2005; Thaker et al. 2011), and invertebrates (Schmitz 2005). Predator avoidance therefore may be the cause of decreased SEA observed at our localities with higher predation pressure. Systematic experiments are required to determine the effect predation pressure has on the foraging behavior of each individual species.

Understanding how ecological factors, such as island size, competition, and predation, influence dietary niche width is critical to forecasting the long-term persistence of species and ensuring their effective management and conservation. The Alexander Archipelago of southeastern Alaska is host to numerous endemic taxa, which have been or potentially will be threatened by a variety of anthropogenic impacts, such as habitat fragmentation and conversion, introduction of exotic species and pathogens, and climate change (Cook and MacDonald 2001; Dawson et al. 2007; Weckworth et al. 2015). Our analyses produced only a minimum estimate of niche overlap between the study species across localities. Despite this, our study demonstrates the complexity of species interactions, including variability in dietary niche breadth as well as the potential impact of competition and predation. We encourage that specimens acquired from future trapping efforts within this archipelago be utilized for stable isotope analyses, which could then be combined with the data presented here to provide a more comprehensive picture of species interactions across the Alexander Archipelago. Because species interactions and individual foraging decisions are not static, this complex island system requires management protocols based on an understanding of how species interactions, habitat use, and forest management influence these mammalian communities to ensure their long-term persistence within southeastern Alaska.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—List of localities sampled—comprehensive list of island and mainland localities, including island sizes, distance to mainland, specific locality names, latitude–longitude, species sampled, specimen totals ($n = 340$), and the number of potential mammalian competitors and predators at each locality in the Alexander Archipelago and adjacent Alaskan mainland.

Supplementary Data SD2. Specimen catalog—comprehensive list of specimens used, including museum catalog numbers, general locality, species, count and type of postcranial bone sampled for stable isotope analysis, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and date specimen was collected.

Supplementary Data SD3. Competitor references—sources used for dietary information to determine potential competitor status of each species.

Supplementary Data SD4. Competitor and predator species—species of potential small mammal competitors and mammalian predators at each locality.

Supplementary Data SD5. Isotopic niche data— isotopic niche width (SEAB and SEAC in ‰²) versus the level of competition (A) and predation (B) by locality size.

LITERATURE CITED

- AMBROSE, S. H., AND L. NORR. 1992. On stable isotopic data and prehistoric subsistence in the Soconusco region. *Current Anthropology* 33:401–404.
- ARAÚJO, M. S., D. I. BOLNICK, AND C. A. LAYMAN. 2011. The ecological causes of individual specialisation. *Ecology Letters* 14: 948–958.
- ARCTOS. 2015. Arctos: collaborative collection management solution. <http://arctos.database.museum/>. Accessed April 2015–October 2015.
- BARBEHENN, K. R. 1958. Spatial and population relationships between *Microtus* and *Blarina*. *Ecology* 39:293–304.
- BARNARD, C. J., C. A. J. BROWN, AND J. GRAY-WALLIS. 1983. Time and energy budgets and competition in the common shrew (*Sorex araneus* L.). *Behavioral Ecology and Sociobiology* 13:13–18.
- BEARHOP, S., C. E. ADAMS, S. WALDRONS, R. A. FULLER, AND H. MACLEOD. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73:1007–1012.

- BOLNICK, D. I., ET AL. 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* 161:1–28.
- BOND, A. L., T. D. JARDINE, AND K. A. HOBSON. 2016. Multi-tissue stable-isotope analyses can identify dietary specialization. *Methods in Ecology and Evolution* 7:1428–1437.
- BUCKLEY, L. B., AND J. ROUGHGARDEN. 2006. Climate, competition, and the coexistence of island lizards. *Functional Ecology* 20:315–322.
- CARPENTER, S. R., ET AL. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876.
- CARRARA, P. E., T. A. AGER, AND J. F. BAICHTAL. 2007. Possible refugia in the Alexander Archipelago of southeastern Alaska during the late Wisconsin glaciation. *Canadian Journal of Earth Sciences* 44:229–244.
- CHURCHFIELD, S. 1994. Foraging strategies of shrews, and the evidence from field studies. Pp. 77–87 in *Advances in the biology of shrews*. Special Publication of the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.
- CONROY, C. J., J. R. DEMBOSKI, AND J. A. COOK. 1999. Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. *Journal of Biogeography* 26:343–352.
- COOK, J. A., N. G. DAWSON, AND S. O. MACDONALD. 2006. Conservation of highly fragmented systems: the north temperate Alexander Archipelago. *Biological Conservation* 133:1–15.
- COOK, J. A., AND S. O. MACDONALD. 2001. Should endemism be a focus of conservation efforts along the North Pacific Coast of North America? *Biological Conservation* 97:207–213.
- COOK, J. A., AND S. O. MACDONALD. 2013. Island life: coming to grips with the insular nature of the North Pacific coastal forests. Pp. 19–42 in *North Pacific temperate rainforests: ecology and conservation* (G. H. Orians and J. W. Schoen, eds.). University of Washington Press, Seattle.
- DARIMONT, C. T., P. C. PAQUET, AND T. E. REIMCHEN. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *The Journal of Animal Ecology* 78:126–133.
- DAWSON, N. G., S. O. MACDONALD, AND J. A. COOK. 2007. Endemic mammals of the Alexander Archipelago. Pp. 1–11 In *The coastal forest and mountains ecoregion of southeastern Alaska and the Tongass National Forest: a conservation assessment and resource synthesis*, Chapter 6.7 (J. W. Schoen and Dovichin, eds.). Audubon Alaska and The Nature Conservancy, Anchorage.
- DOYLE, A. T. 1990. Use of riparian and upland habitats by small mammals. *Journal of Mammalogy* 71:14–23.
- FEY, K., P. B. BANKS, AND E. KORPIMÄKI. 2008. Voles on small islands: effects of food limitation and alien predation. *Oecologia* 157:419–428.
- FULK, G. W. 1972. The effect of shrews on the space utilization of voles. *Journal of Mammalogy* 53:461–478.
- GENOUD, M. 1985. Ecological energetics of two European shrews: *Crocidura russula* and *Sorex coronatus* (Soricidae: Mammalia). *Journal of Zoology* 207:63–85.
- GRANT, P. R. 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society* 4:39–68.
- HAMILTON, JR., W. J. 1930. The food of the Soricidae. *Journal of Mammalogy* 11:26–39.
- HANSKI, I., AND H. HENTTONEN. 1996. Predation on competing rodent species: a simple explanation of complex patterns. *Journal of Animal Ecology* 65:220–232.
- HARDIN, G. 1960. The competitive exclusion principle. *Science* 131:1292–1297.
- HEBBLEWHITE, M., E. H. MERRILL, AND T. L. McDONALD. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos* 111:101–111.
- HOLMES, W. G. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. *Behavioral Ecology and Sociobiology* 15:293–301.
- HOLT, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–129.
- HOPE, A. G., ET AL. 2016. Revision of widespread red squirrels (genus *Tamiasciurus*) highlights the complexity of speciation within North American forests. *Molecular Phylogenetics and Evolution* 100:170–182.
- JACKSON, A. L., R. INGER, A. C. PARNELL, AND S. BEARHOP. 2011. Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. *The Journal of Animal Ecology* 80:595–602.
- KOTLER, B. P. 1984. Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701.
- KOTLER, B. P., J. S. BROWN, AND O. HASSON. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260.
- LEVINE, H. J. 1997. Rest heart rate and life expectancy. *Journal of the American College of Cardiology* 30:1104–1106.
- LIMA, S. L. 1998. Nonlethal effects in the ecology of predator-prey interaction. *BioScience* 48:25–34.
- LIMA, S. L. 2002. Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution* 17:70–75.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decision made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- LISTER, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. *Evolution* 30:659–676.
- LOMOLINO, M. V. 1984. Immigrant selection, predation, and the distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. *The American Naturalist* 123:468–483.
- MACARTHUR, R. H., J. M. DIAMOND, AND J. R. KARR. 1972. Density compensation in island faunas. *Ecology* 53:330–342.
- MACDONALD, S. O. AND J. A. COOK. 2007. *The Mammals and Amphibians of Southeast Alaska*. Museum of Southwestern Biology, Special Publication 8, 191 pp. University of New Mexico, Albuquerque, NM.
- MACDONALD, S. O. AND J. A. COOK. 2009. *Recent mammals of Alaska*. University of Alaska Press, Fairbanks.
- MARTINEZ DEL RIO, C., N. WOLF, S. A. CARLETON, AND L. Z. GANNES. 2009a. Isotopic ecology ten years after a call for more laboratory experiments. *Biological Reviews* 84:91–111.
- MARTINEZ DEL RIO, C., P. SABAT, R. ANDERSON-SPRECHER, AND S. P. GONZALEZ. 2009b. Dietary and isotopic specialization: the isotopic niche of three *Cinclodes* ovenbirds. *Oecologia* 161:149–159.
- MASSON, J. F. K. 1975. Stomach content analysis of mullet from the Swartkop Estuary. *African Zoology* 10:193–207.
- MUSTONEN, A. M., S. SAARELA, AND P. NIEMINEN. 2008. Food deprivation in the common vole (*Microtus arvalis*) and the tundra vole (*Microtus oeconomus*). *Journal of Comparative Physiology, B: Biochemical, Systemic, and Environmental Physiology* 178:199–208.
- NEWSOME, S. D., C. MARTINEZ DEL RIO, S. BEARHOP, AND D. L. PHILLIPS. 2007. A niche for isotopic diversity. *Frontiers in Ecology and the Environment* 5:429–436.

- OCHOCIŃSKA, D., AND J. R. TAYLOR. 2005. Living at the physiological limits: field and maximum metabolic rates of the common shrew (*Sorex araneus*). *Physiological and Biochemical Zoology* 78:808–818.
- OKSANEN, J., ET AL. 2017. vegan: community ecology package. R package version 2.4-4. <https://CRAN.R-project.org/package=vegan>. Accessed September 2017.
- PAINE, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* 100:65–75.
- PARNELL, A., AND A. JACKSON. 2013. siar: stable isotope analysis in R. R package version 4.2.2. <https://CRAN.R-project.org/package=siar>. Accessed May 2017.
- PECKARSKY, B. L., ET AL. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* 89:2416–2425.
- R DEVELOPMENT CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://R-project.org>. Accessed August 2017.
- REICH, L. M. 1981. *Microtus pennsylvanicus*. *Mammalian Species* 159:1–8.
- ROBINSON-WOLRATH, S. I., AND I. P. OWENS. 2003. Large size in an island-dwelling bird: intraspecific competition and the dominance hypothesis. *Journal of Evolutionary Biology* 16:1106–1114.
- ROUGHGARDEN, J. 1972. Evolution of niche width. *The American Naturalist* 106:683–718.
- ROUGHGARDEN, J. 1974. The fundamental and realized niche of a solitary population. *The American Naturalist* 108:232–235.
- SANTOS, A. M. C., R. FIELD, AND R. E. RICKLEFS. 2016. New directions in island biogeography. *Global Ecology and Biogeography* 25:751–768.
- SAWYER, Y. E., AND J. A. COOK. 2016. Phylogeographic structure in long-tailed voles (Rodentia: Arvicolinae) belies the complex Pleistocene history of isolation, divergence, and recolonization of northwest North America's fauna. *Ecology and Evolution* 6:6633–6647.
- SCHMITZ, O. J. 2005. Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management. *Oecologia* 145:225–234.
- SCOTT, S. N., S. M. CLEGG, S. P. BLOMBERG, J. KIKKAWA, AND I. P. OWENS. 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. *Evolution* 57:2147–2156.
- SMITH, M. E., AND M. C. BELK. 1996. *Sorex monticolus*. *Mammalian Species* 528:1–5.
- SMOLEN, M. J., AND B. L. KELLER. 1987. *Microtus longicaudus*. *Mammalian Species* 271:1–7.
- TAITT, M. J., J. H. W. GIPPS, C. J. KREBS, AND Z. DUNDJERSKI. 1981. The effect of extra food and cover on declining populations of *Microtus townsendii*. *Canadian Journal of Zoology* 59:1593–1599.
- TAYLOR, J. R. E. 1998. Evolution of energetic strategies in shrews. Pp. 309–346 in *Evolution of shrews* (J. M. Wojcik and M. Wolsan, eds.). Mammal Research Institute, Białowieża, Poland.
- THAKER, M., A. T. VANAK, C. R. OWEN, M. B. OGDEN, S. M. NIEMANN, AND R. SLOTOW. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* 92:398–407.
- VAN VALEN, L. 1965. Morphological variation and width of ecological niche. *The American Naturalist* 99:377–390.
- WECKWORTH, B. V., N. G. DAWSON, S. L. TALBOT, AND J. A. COOK. 2015. Genetic distinctiveness of Alexander Archipelago wolves (*Canis lupus ligoni*). *The Journal of Heredity* 106:412–414.
- WHITAKER, JR., J. O. 1966. Food of *Mus musculus*, *Peromyscus maniculatus bairdi* and *Peromyscus leucopus* in Vigo County, Indiana. *Journal of Mammalogy* 47:473–486.
- WHITAKER, JR., J. O. 2004. *Sorex cinereus*. *Mammalian Species* 743:1–9.

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