Feeding preference and diet overlap at different taxonomic scales: the implications for coexistence of two small herbivores

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Dietary niche separation is often crucial for promoting coexistence of sympatric species sharing similar habitats. In this study, we used cafeteria experiments to explore feeding preferences of two sympatric small herbivores in Hulunber meadow steppe, the narrow-headed vole (*Microtus gregalis*) and the Daurian pika (*Ochotona dauurica*), and used microhistological analysis of stomach contents to measure their actual diets and evaluate their niche overlap. To evaluate the effects of scale, we conducted dietary analyses at two commonly documented taxonomic scales of food type categorization: a fine scale based on the species level, and a coarse scale based on a roughly family-level categorization. Niche analysis at the fine and the coarse scales generated qualitatively similar results, although niche overlap was larger at the coarse scale than at the fine scale. In cafeteria experiments, voles and pikas showed similar feeding preference patterns. When foraging in the field, the two species differed in food use and feeding preference, without a significant dietary niche overlap. In the laboratory, both species preferred to eat Leguminosae and Asteraceae species. In the field, pikas still preferred Leguminosae species and voles switched to prefer Liliaceae species. These results suggest the existence of dietary niche partitioning, and competition might have driven the observed niche shift.

Key words: diet, niche overlap, niche partitioning, pika, taxonomic scale, vole

Understanding how sympatric species manage to coexist is a central task for community ecologists (Chesson 2000). According to the competitive exclusion principle, absolute competitors cannot coexist stably and niche partitioning or separation is generally required for long-term coexistence (Hardin 1960; MacArthur and Levins 1967; Pianka 1969). Habitat (spatial niche), food (dietary niche), and time (temporal niche) have long been considered as the three major niche dimensions that are partitioned by competing species (Schoener 1974). The role of dietary niche partitioning is generally important across communities and may be even more crucial for sympatric species inhabiting similar habitats, as suggested by the hypothesis of niche complementarity (Schoener 1974). It is therefore not surprising that many efforts have been made to find differences in diets among sympatric species (Page et al. 2005; Sutherland 2011; Ramesh et al. 2012; Symes et al. 2013).

However, mere presence of a difference in diets does not necessarily imply the existence of competition, since differences may simply arise from random use of resources, or remain the same with or without competition (Schoener 1974). Computation-intensive techniques such as bootstrap or permutation tests offer a convenient approach to test the significance of niche overlap (Gotelli et al. 2015). To evaluate the role of competition in shaping diets, ecologists often resort to manipulative experiments or natural experiments to compare the diets of the same species with and without the presence of putative competitors (Brabrand 1985; Persson and Hansson 1999; Landman et al. 2013). Niche parameters, such as niche breadth and niche overlap index, are often measured. If diets play a role in reducing competition, we expect shifts in diets and lower dietary niche overlaps with the presence of competitors.

Moreover, one should also be cautious in evaluating the values of niche breadth and niche overlap, since such niche parameters are often sensitive to how resource states or resource types are defined (Krebs 1999). Significant niche overlap at one taxonomic scale of resources consumed (e.g., species versus families of plants consumed by herbivores) does not necessarily mean similar results at another scale (Shipley et al. 2009). Since animals may not perceive food types as ecologists do, it is better to conduct multiscale analyses of diets and compare results obtained at different scales. However, to the best of our knowledge, such multiscale studies are scarce.

In the present study, we explore the diets of two small herbivores inhabiting a meadow steppe and evaluate the role of diet partitioning on coexistence. This system features a smaller-sized herbivore, the narrow-headed vole (*Microtus gregalis*) and a larger-sized herbivore, the Daurian pika (*Ochotona dauurica*), both strictly herbivorous (Wang et al. 2001; Smith and Xie 2008). Previous trapping records suggest that the two species have similar habitat preferences and activity patterns (Ren 2010; Cao et al. 2016), which highlights the potential importance of dietary niche partitioning. We carried out the study in early autumn, when both species reached their peaks in population density (Ren 2010) and may thus encounter the most intensive interspecific competition. For each species, we explored its intrinsic feeding preference by using cafeteria experiments and its actual diet in the field by using microhistological analysis of stomach contents. We then measured the dietary niche overlap between the two species and evaluated its significance by using permutation tests. According to the hypothesis of niche complementarity, we predict that the two species should not indicate significant dietary niche overlap in the field and significantly differ in patterns of food use. Moreover, our dietary niche analyses were carried out at two taxonomic scales of categorization commonly used by ecologists, with a fine scale based on individual plant species, and a coarse scale based on a roughly family-level categorization.

Materials and Methods

Study area.—We carried out the study at the Xiertala farm (49°19′ N, 120°03′ E) in Hulunber meadow steppe, northeastern China. The climate at the study site is generally continental, characterized by a wet, warm summer and a severe, long winter. The monthly average temperature ranges from −25°C (January) to 19°C (July). The annual mean rainfall is about 250 mm, peaking in July to early September. The vegetation at the study site was dominated by *Leymus chinensis*, *Stipa baicalensis*, *Carex pediformis*, *Galium verum*, and *Bupleurum scorzonerifolium*, with accompanying species like *Astragalus adsurgens*, *Vicia amoena*, and *Poa pratensis* (Yan et al. 2016).

Availability of food resources.—To assess food availability, we conducted a vegetation survey 1 day before our live-trapping. Twenty 1 × 1 m^2 quadrats were randomly selected (spacing > 10 m) within the trapping area. We recorded the coverage (by visual estimation) and dry weight (by clipping and weighing) for each plant species found within each quadrat, and the

species with mean coverage greater than 0.5% were considered to be available food resources for voles and pikas. According to this criterion, a total of 40 plant species were selected for the subsequent experiments.

Measurements of niche breadth and niche overlap were carried out at two scales of categorization. At the fine scale, each of the 40 plant species was viewed as a distinct food type, and its availability was represented by its average proportional dry weight. At the coarse scale, the 40 species were grouped into seven roughly family-level types: Type 1: Grass (including seven Poaceae, two Cyperaceae, and one Iridaceae, representing ca. 45.7% of total dry weight); Type 2: Asteraceae (six species, ca. 6.4% of total dry weight); Type 3: Leguminosae (eight species, ca. 19.2% of total dry weight); Type 4: Ranunculaceae (four species, ca. 19.8% of total dry weight); Type 5: Liliaceae (four species, ca. 2.2% of total dry weight); Type 6: Rosaceae (three species, ca. 2.2% of total dry weight); and Type 7: the others (including two Apiaceae, one Rubiaceae, one Campanulaceae, and one Caryophyllaceae, ca. 4.4% of total dry weight). For each type, we used its average proportional dry weight as a surrogate of its relative availability.

Animal preparation.—To avoid potential effects of disturbance like cattle grazing and mowing, animals used in this study were all trapped from a permanent cattle-proof enclosure (ca. 34 ha), operated by the Hulunber Grassland Ecosystem Observation and Research Station, Chinese Academy of Agricultural Sciences. Trapping was carried out during August in 2014. We selected a roughly rectangular area (ca. 12 ha) in the central area of the enclosure to conduct livetrapping. In this area, we arranged five transects spaced 50 m apart, with each transect consisting of 50 trapping stations set at 10-m intervals. At each trapping station, we placed a collapsible wire cage (12 × 15 × 30 cm, locally made) baited with fried peanuts. We checked cages three times per day (dawn, noon, and dusk) and rebaited the cages when necessary. The trapping session lasted for 4 consecutive days. Only adults were included in our study and all juveniles captured were released upon capture (voles heavier than 20 g and pikas heavier than 50 g were considered to be adults). The adults captured in days 1 and 3 were sacrificed with ether and dissected (a total of 24 voles and 11 pikas), with their stomachs preserved in formalin for later diet analysis. The other adults were maintained in our laboratory and later subjected to the cafeteria experiments (a total of 15 voles and 9 pikas). Our husbandry and experimental procedures followed the guidelines approved by the American Society of Mammalogists (Sikes et al. 2016).

Cafeteria experiments and feeding preference analysis.—We adopted indoor cafeteria experiments to measure intrinsic dietary preference of animals in the absence of competition and predation risk. During this experiment, the subject animals were housed separately in cylindrical plastic vats (measuring 45 cm in diameter and 95 cm tall) under natural photoperiod and a roughly constant temperature (ca. 18°C). Before each session, the animals were deprived of food for 12 h but with access to ad lib drinking water. The 40 plant species considered to be available food resources were collected from the trapping area and randomly

arranged into five groups. The experiment consists of five sessions per individual. In each session, eight different plant species (one group) of similar weight (ca. 5 g) were provided on separate plastic disks (ca. 10 cm in diameter) spaced 5 cm apart. Each session started within 10 min of the time that the plants were collected. The animal then had free access to these food items for 2 h. We recorded the weight of each food type before and after each session. According to Manly et al. (1993), the preference index (w) or selection index for food type i can be represented as

$$w_i = \frac{r_i}{n_i},$$

where r_i represents proportional weight of food type i in the diet and n_i represents proportional weight of food type i available. To adjust for the effects of dehydration, a comparable sample from each food type was synchronously maintained in another similar vat (in the absence of foragers) during each session, enabling us to measure dehydration rate of each food type.

Analysis of stomach contents.—We employed microhistological analysis of stomach contents to explore the actual food use of animals in their natural environment. In preparing the sample slides and the reference slides required by this method, we followed the procedures described by Sparks and Malechek (1968). Contents from each stomach were thoroughly mixed with distilled water and washed over a 200-mesh screen for 4–5 times. The oversized fragments were oven-dried under 65°C for 24 h and then ground over a 1-mm screen. The fragments passing through the screen were therefore of roughly similar size. We stained these fragments using 1% hematoxylin and then mounted a small portion of the stained fragments on a slide to create a sample slide. We also collected fresh tissues from each of the 40 plant species by using scalpels and prepared them as reference slides in the same manner. For each individual animal, five sample slides were prepared and then observed under a compound binocular microscope (100 × magnification). For each sample slide, we systematically selected 20 views for observation. We identified the plant species in each view according to the reliable epidermal features suggested by the reference slides. For each species, proportional frequency of occurrence for a given food type was used as the measure of relative food use. For food type i, its proportional frequency of occurrence was calculated as its frequency of occurrence (the number of views containing at least one fragment of a certain food type across all the views) divided by total frequency of occurrence for all the food types (Holechek and Gross 1982).

Diet analysis and measurement of niche parameters.—We used Levins' standardized index to measure dietary niche breadth of voles and pikas. For each species, the Levins' standardized index was calculated as follows:

$$B = \left(\frac{1}{\sum P_i^2} - 1\right)/(n-1),$$

where P_i is the proportional frequency of occurrence for food type i in the diet of the focus species, and n is the number of food types. B ranges from 0 to 1, with 0 indicating an absolute

specialist and 1 indicating an absolute generalist (Hurlbert 1978).

Similar to the cafeteria experiment, we calculated a selection index (w_f) using results of stomach contents analysis at both scales, with r_i representing proportional frequency of occurrence for food type i in the diet of the focus species and n_i representing average proportional dry weight of food type i available in the environment. According to Holechek and Gross (1982), proportional frequency of occurrence is generally a good surrogate for dry weight composition of a mixture sample.

The dietary overlap between voles and pikas was measured by the Pianka overlap index as follows:

$$O_{ij} = \frac{\sum_{i=1}^{n} P_{ij}P_{ik}}{\sqrt{\sum_{i=1}^{n} P_{ij}^2 \ \sum_{i=1}^{n} P_{ik}^2}},$$

where P_{ij} and P_{ik} are the proportional frequencies of occurrence for food type i in the diet of species j and k, respectively. Similarly, the index O_{jk} ranges from 0 to 1, with 0 representing total diet partitioning and 1 represent total diet overlap (Pianka 1973). To test the significance of diet overlap, we used the function *niche_null_model* in R package *EcoSimR* (Gotelli et al. 2015), which compared the observed overlap index with simulated values generated by randomizing the original resource utilization matrix for 1,000 iterations. The default randomization algorithm (*RA3*) of *EcoSimR* was adopted. As an alternative to diet overlap, we used a contingency table analysis on frequency of occurrence to evaluate whether the two species differ significantly in food utilization pattern. For both cafeteria experiments and field experiments, we employed correlation analyses on the selection index to evaluate how similarly pikas and voles preferred food items. For each species, we also used correlation analyses on the selection index to evaluate whether food preference was similar between the cafeteria and field experiments. Niche overlap assessments, contingency table analyses, and correlations were all conducted at both taxonomic scales. We conducted all the statistical work on the R platform version 3.1.3 (R Core Team 2018).

RESULTS

Cafeteria experiments.—The cafeteria experiments (Table 1) showed that pikas and voles fed on all of the 40 plant species. Pikas preferred 13 species and voles preferred 11 species, with 7 species preferred by both. The three most-preferred food types were *Taraxacum mongolicum* ($w = 4.14$), *Scorzonera divaricata* ($w = 2.44$), and *Bupleurum chinense* ($w = 2.42$) for pikas; and *S. divaricata* ($w = 8.93$), *T. mongolicum* ($w = 3.58$), and *Gueldenstaedtia verna* ($w = 2.77$) for voles. At the coarse scale (Fig. 1A), pikas preferred to feed on Leguminosae species ($w = 1.45$) and least preferred to feed on Grass ($w = 0.75$), while voles preferred to feed on Asteraceae species ($w = 1.57$) and least preferred to feed on Rosaceae species ($w = 0.44$). The correlation analysis on the selection index (w) suggested that in the cafeteria experiment,

Table 1.—Dietary preference of voles (*Microtus gregalis*) and pikas (*Ochotona dauurica*) under laboratory and field conditions. n_i = proportions of food species *i* available; w_i = Selection index for food species *i*. A food was preferred when $w_i > 1$ (bolded numbers), and avoided when $w_i < 1$. Note that in the field experiments, n_i is the same for voles and pikas.

Plant species	Cafeteria experiment				Field experiment		
	Vole		Pika		Vole		Pika
	n_i	w_i	n_i	w_i	n_i	w_i	w_i
Grass							
Leymus chinensis	0.029	0.477	0.027	0.757	0.171	0.254	**1.062**
Stipa baicalensis	0.030	0.747	0.027	0.571	0.023	0.671	**2.818**
Cleistogenes squarrosa	0.021	**1.488**	0.019	0.976	0.010	0.864	**5.598**
Carex pediformis	0.022	0.580	0.022	0.946	0.071	0.000	0.523
C. duriuscula	0.026	0.479	0.023	**1.082**	0.058	0.125	0.000
Koeleria cristata	0.027	0.838	0.025	0.952	0.014	**2.639**	**2.699**
Poa annua	0.026	0.699	0.023	0.819	0.005	0.344	0.000
Festuca ovina	0.022	0.848	0.023	0.573	0.016	0.722	**1.143**
Achnatherum sibiricum	0.024	0.537	0.025	0.562	0.036	0.250	0.213
Iris ventricosa	0.021	**1.444**	0.021	0.265	0.052	0.000	0.063
Leguminosae							
Serratula chinensis	0.032	0.743	0.032	0.877	0.039	0.768	**3.372**
Taraxacum mongolicum	0.021	**3.575**	0.022	**4.135**	0.009	0.981	0.000
Artemisia frigida	0.026	0.438	0.025	0.977	0.009	0.194	0.000
A. dracunculus	0.027	0.567	0.026	0.661	0.015	0.769	**6.540**
A. tanacetifolia	0.030	0.710	0.031	0.766	0.102	0.044	0.119
Scorzonera divaricata	0.013	**8.928**	0.012	**2.444**	0.002	**20.264**	0.000
Heteropappus altaicus	0.028	0.628	0.029	**1.332**	0.004	**2.692**	**6.515**
Tephroseris kirilowii	0.040	0.254	0.041	0.371	0.014	0.000	0.000
Ranunculaceae							
Pulsatilla turczaninovii	0.027	0.846	0.025	0.751	0.062	0.544	0.479
Clematis hexapetala	0.031	0.423	0.030	0.659	0.005	**3.268**	**1.917**
Thalictrum squarrosum	0.025	0.694	0.028	0.349	0.127	0.776	0.302
T. petaloideum	0.019	**1.601**	0.022	**1.560**	0.003	0.000	0.000
Asteraceae							
Astragalus adsurgens	0.014	0.300	0.018	0.907	0.002	0.000	**4.473**
A. melilotoides	0.010	**2.485**	0.011	**1.727**	0.029	0.250	0.000
Vicia amoena	0.020	0.726	0.022	**1.973**	0.009	0.977	**5.613**
V. cracca	0.026	**1.428**	0.028	**1.568**	0.009	0.850	**8.307**
Oxytropis myriophylla	0.025	0.754	0.025	**1.191**	0.014	**11.807**	**1.038**
Gueldenstaedtia verna	0.010	**2.769**	0.010	**1.330**	0.002	0.000	0.000
Liliaceae							
Allium tenuissimum	0.030	0.508	0.033	0.785	0.004	**10.851**	**1.022**
A. ramosum	0.026	0.811	0.024	**1.591**	0.001	**32.030**	0.000
A. bidentatum	0.032	**1.295**	0.032	0.880	0.014	**11.399**	**1.038**
Lilium pumilum	0.028	0.950	0.029	0.840	0.003	**3.268**	0.000
Rosaceae							
Potentilla bifurca	0.020	0.483	0.020	**1.102**	0.011	**6.091**	0.775
P. tanacetifolia	0.026	0.584	0.024	0.857	0.010	**2.593**	0.634
P. acaulis	0.024	0.243	0.021	0.378	0.001	**1.868**	0.000
Others							
Bupleurum chinense	0.026	**1.417**	0.025	**2.419**	0.005	**6.424**	**8.593**
Adenophora stricta	0.030	**2.438**	0.029	0.801	0.017	**1.039**	0.000
Saposhnikovia divaricata	0.029	0.868	0.031	0.628	0.002	**13.400**	**10.223**
Galium verum	0.020	0.707	0.022	0.837	0.020	0.870	0.439
Dianthus chinensis	0.040	0.654	0.041	0.603	0.001	0.000	0.000

the two species showed moderately similar preferences at the fine scale, and quite similar patterns of feeding preference at the coarse scale (fine scale: Spearman's rank correlation coefficient = 0.42, $P < 0.01$; coarse scale: Spearman's correlation coefficient = 0.96, $P < 0.001$).

Field experiments.—At the fine scale (Table 1), pikas fed on 26 and voles fed on 33 out of 40 plant species. However, given such diverse diets, the dietary niche breadths of both species were relatively small (the observed values were 0.28 for pika and 0.30 for vole, while the theoretically maximum values were 0.64 for pika and 0.82 for vole), suggesting that both species are somewhat selective among food types. According to the

criterion of selection index larger than 1, pikas preferred 17 species and voles preferred 15 species. Among these, *Saposhnikovia divaricata* (w_f = 10.22), *Bupleurum chinense* (w_f = 8.59), and *Vicia cracca* (w_f = 8.31) were the three highly preferred species for pikas, while voles mostly preferred to eat *Allium ramosum* (w_f = 32.03), *Scorzonera divaricata* (w_f = 20.26), and *Saposhnikovia divaricata* (w_f = 13.40). The correlation analysis on the selection index in the field (w_f) suggested there was no significant correlation between food selection of pikas and voles (Spearman's rank correlation coefficient = 0.29, $P = 0.07$).

At the coarse scale, the dietary niche breadths were larger for both species, but to different extents (the observed values
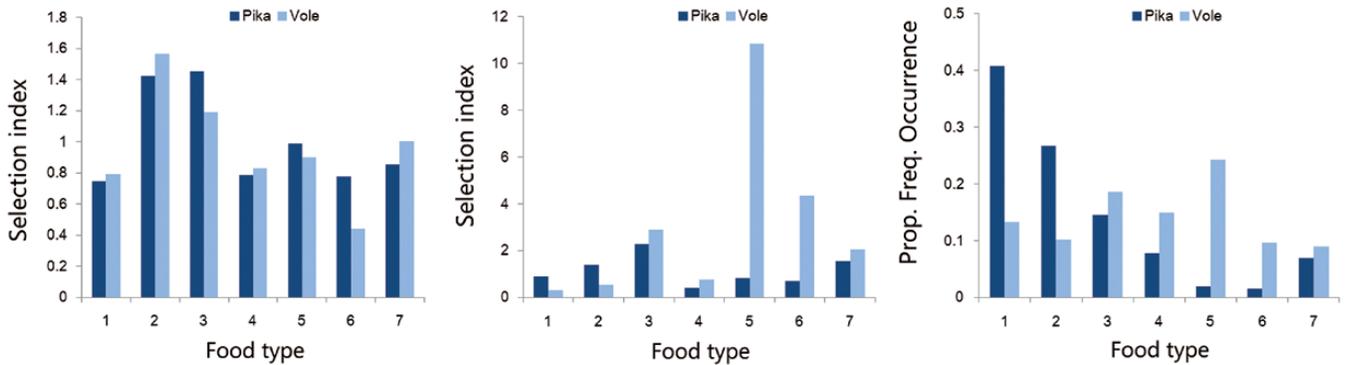
Figure 1.—Comparison of food use between pikas (*Ochotona dauurica*) and voles (*Microtus gregalis*) at the coarse taxonomic scale of food type categorization. Horizontal axis represents food types based on a roughly family level (1: Grass; 2: Asteraceae; 3: Leguminosae; 4: Ranunculaceae; 5: Liliaceae; 6: Rosaceae; and 7: the others). Vertical axes represent (A) selection index obtained from cafeteria experiments (9 pikas and 15 voles); (B) selection index obtained from field experiments (11 pikas and 24 voles); and (C) proportional frequency of occurrence according to the microhistological analysis on stomach contents (11 pikas and 24 voles). Data were collected at the Xiertala farm, Inner Mongolia, China during August 2013.
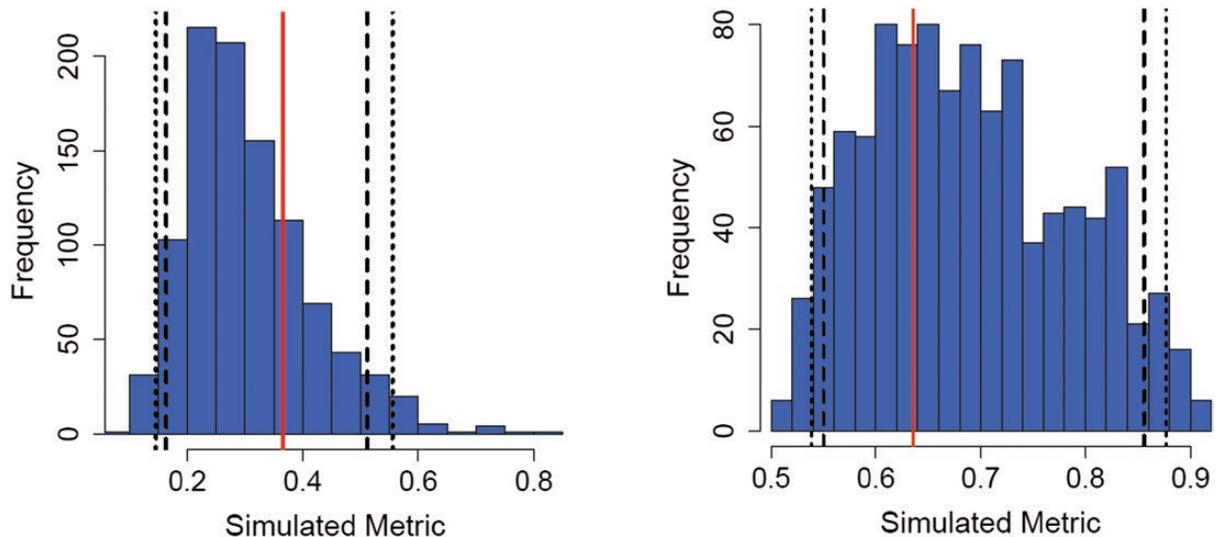
Figure 2.—Histograms for permutation tests on Pianka dietary niche overlap between pikas (*Ochotona dauurica*, n = 11) and voles (*Microtus gregalis*, n = 24). Left: Niche overlap on the fine taxonomic level with each separate plant species defined as a distinct food type. Right: Niche overlap on the coarse taxonomic level with food type categorization based on a roughly family level. Vertical lines represent observed values of niche overlap. Pairs of vertical dashed lines represent the boundaries of the one-tailed (long dash) and the two-tailed (short dash) 95% confidence intervals. Data were collected at the Xiertala farm, Inner Mongolia, China during August 2013.

were 0.45 for pika and 0.87 for voles, while the theoretically maximum values were 1 for both). According to the selection index (Fig. 1B), the most preferred food type for pikas was Leguminosae (Type 3, $w_f = 2.26$), followed by Type 7 ($w_f = 1.56$) and Asteraceae (Type 2, $w_f = 1.39$). For voles, Liliaceae (Type 5, $w_f = 10.85$) was the most preferred, followed by Rosaceae (Type 6, $w_f = 4.35$), Leguminosae (Type 3, $w_f = 2.90$), and Type 7 ($w_f = 2.03$). Again, no significant correlation between food selection of pikas and voles was detected (Spearman correlation coefficient $= -0.11$, $P = 0.82$). In terms of proportional frequency of occurrence (Fig. 1C), Grass (Type 1, 40.72%) constituted the largest part of the diet of pikas, followed by Asteraceae (Type 2, 26.67%) and Leguminosae (Type 3, 14.59%). By contrast, voles mainly fed on Liliaceae (Type 5, 24.20%), Leguminosae (Type 3, 18.59%), and Ranunculaceae (Type 4, 14.94%).

Chi-square tests on frequency of occurrence suggest that the two herbivores significantly differed in diets when foraging in the field, regardless of scale of categorization (fine scale: $\chi^2 = 1133.04$, *d.f.* = 35, *P* < 0.001; coarse scale: $\chi^2 = 575.02$, *d.f.* = 6, *P* < 0.001). The dietary niche overlap between pikas and voles increased with the increasing scale of categorization (fine scale: *O* = 0.37; coarse scale: *O* = 0.64). However, permutation tests (Fig. 2) suggest that dietary niche overlap was not significant at either the fine scale (*P* = 0.25) or the coarse scale (*P* = 0.67). Correlation analyses also suggest that for both species, there was no significant correlation between the selection index obtained from cafeteria experiments and that from field experiments (pika: Spearman correlation coefficient = 0.01, *P* = 0.98; vole: Spearman correlation coefficient = 0.17, *P* = 0.29).

DISCUSSION

In this study, we explored the dietary niches of two sympatric herbivores at multiple scales, as well as niche overlap between them. Food use and feeding preference were measured both by cafeteria and field experiments. As predicted, dietary overlap was not significant in the field experiment. Pikas and voles showed similar food-preference patterns in cafeteria experiments but distinct patterns in the field experiments. Niche overlap and similarity in food preference were larger at the coarse scale than at the fine scale. However, analyses at the fine and the coarse scales gave qualitatively similar assessments. Taken together, these results support the hypothesis that dietary niche partitioning facilitates coexistence of these two species.

Consistent with some previous studies (Dearing 1996), pikas and voles in our study system can be roughly viewed as dietary generalists. In the field study, of the 40 available plant species, pikas ate 26 plant species and voles ate 33 plant species. In the cafeteria experiments, all of the 40 plant species were foraged to some extent by both species. The ability to feed on a wide range of food types has an obvious advantage in reducing foraging time, which is crucial for these small herbivores since they often face high predation risk when foraging. Such a feeding style may also bring benefits in nutrient balancing since food resources are often imperfectly substitutable (Pulliam 1975; Rapport 1980). Moreover, it is suggested that compared to specialists, generalists are less impacted by novel plant secondary metabolites (Sorensen et al. 2005).

However, there are some prerequisites to becoming a dietary generalist. Some physiological and behavioral traits may contribute to this adaptation. For instance, pikas are well known for their food-hoarding behavior. In early autumn, they usually make haypiles for future use besides immediate consumption (L-Y. Shuai, pers. obs.). As many toxins (such as terpenes and some phenols) contained in plants are volatile, such a food-caching strategy may be beneficial in reducing the amount of toxins before consumption (Dearing 1997). This would enable foragers to utilize plant species containing high levels of toxic secondary compounds, which are typically avoided by mammalian herbivores (Dearing 1997; Torregrossa and Dearing 2009). Food-caching behavior is also common in voles and may play a similar role in broadening their diets (Nanus and Range 2001; Zhong et al. 2007).

While voles and pikas in the present study possessed broad diets, both species were selective to some extent. Consistent with some previous studies (Batzli and Cole 1979; Lindroth and Batzli 1984; Zhong et al. 2008), both pikas and voles intrinsically preferred dicots to monocots (Fig. 1A), which is reasonable since dicots are generally more digestible than monocots (Batzli and Cole 1979). According to the Jarman–Bell principle, smaller herbivores should be more selective and prefer food types of higher quality, and larger herbivores should include more low-quality food in their diets (Bell 1971; Jarman 1974). Our results support this principle: pikas (the larger-sized species) intrinsically preferred Leguminosae and Asteraceae (Fig. 1A), but they included a large amount of grasses in their diet (Fig. 1C) when Leguminosae and Asteraceae were less abundant in the field (Table 1). Such a pattern was not observed in voles, the smaller-sized species.

It is well documented that interspecific competition can alter food-use patterns (M'Closkey 1978; Basset and Rossi 1990). If shifts in diet are mainly driven by interspecific competition, the dominant species should largely retain its intrinsic preference and the subdominant one should show a significant diet shift, since competition is generally asymmetric (Basset and Rossi 1990). Pikas and voles in our study showed different patterns of diet switching between the two experiments. In cafeteria experiments, Leguminosae species were the most preferred food type for both pikas and voles. In the field experiments, pikas still preferred Leguminosae species but voles switched to prefer Liliaceae species. Our trapping record suggested that adult pikas were much heavier than adult voles (pika: 95.37 ± 5.68 g; vole: 26.44 ± 0.68 g; mean $\pm$ SE). As larger species are more likely to be dominant in interactions (Gaudet and Keddy 1988), it is possible that pikas outcompeted voles to monopolize the most preferred food type shared by both species (Leguminosae in this case), forcing voles to switch their food preference. Further evidence is required to demonstrate this mechanism.

Although our results support a role for competition in promoting the observed niche shift, the possible effects of other factors cannot be ignored. The two experiments differed in many aspects. First, animals in laboratories are free from competition, predation risk, and dramatic microclimatic variation, and only have rather limited time to forage. Second, availability among food types often greatly differed between the two experiments (Table 1), with animals in cafeteria experiments generally encountering more even distribution of food types. Such a difference in food availability may also cause differences in feeding preference. If density of a highly preferred food is lower than a threshold, then optimal foragers should include some less-preferred food items in their diets, i.e., become less selective (Charnov 1976). This is not the case for our study, since the highly preferred food types in the field experiments (Leguminosae for pikas and Liliaceae for voles) are actually less available than in laboratories (Table 1). However, our assessment of food availability in the field was based on the average values of food abundance obtained from 20 quadrats, ignoring the spatial variation of food abundance, which may significantly affect an animal's perception of food availability. Moreover, animals in the cafeteria experiments only encountered a subset of food types in each session. While foraging in the field, animals may have access to more plant species simultaneously and therefore have better chances to encounter their highly preferred food types. In this scenario, animals may search for their favorite food according to their experience or perceived food availability, rather than the distribution measured by us.

Cafeteria experiments (without competitors) and field experiments (with competitors, and often based on stomach contents analyses) are two frequently used methods of measuring diets. One may think that diets measured in cafeteria experiments refer to the fundamental niche and that diets measured in field experiments refer to the realized niche. However, this

is not necessarily the case. More factors than solely presence of competition should be considered when comparing results obtained from these two experiments. To fully disentangle the effects of methodological difference from the effects of competition, a plausible solution is to conduct manipulative experiments with enclosures (with and without competitors) and perform diet analyses in a single manner, which is the aim of our upcoming work.

Acknowledgments

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