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Effects of Leaf Size on Forage Selection by Collared Pikas, *Ochotona collaris*

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Abstract

We examined the influence of leaf size on forage selection by collared pikas (*Ochotona collaris*) living in alpine meadows in the Yukon Territory, Canada, by comparing the winter diets of individually recognized pikas to the available vegetation within their territories and by conducting cafeteria-style preference experiments. Pikas consistently preferred forage with larger leaves in the cafeteria trials. They also collected larger leaves from deciduous shrubs and graminoid species compared to other plant types such as lichens and evergreen shrubs for their winter diets. Pikas assessed differences in leaf size when selecting their winter diets and this appears to be an energetically efficient foraging strategy for surviving seasonal food scarcity.

Introduction

Foraging theory predicts that most consumers are rate-maximizers and that their diets reflect attempts to fulfill nutritional requirements in light of various constraining factors (Stephens and Krebs, 1986). Herbivores maximize foraging effort by consuming higher quality forage, increasing energy intake rates, or by avoiding toxins. An understanding of how herbivores maximize these energy/effort ratios remains central to understanding forage selection.

Pikas (*Ochotona* spp.) are small mammalian herbivores that provide a useful model for studying foraging theory because their behavior should be determined by a few simple cues (Gliwicz et al., 2006). However, the generality of these potential cues has proven elusive, in part because differences between individuals' diets are frequent and often reflect territory-level variation in forage quality, availability, and morphology (Smith, 1974). Many intrinsic and extrinsic predictors of diet have been tested (Millar and Zwickel, 1972; Smith, 1974; Dearing, 1996; Morrison et al., 2004; Gliwicz et al., 2006; Morrison and Hik, 2008). Millar and Zwickel (1972) and Huntly et al. (1986) independently proposed the plant morphology hypothesis, and predicted that central-place foragers, like pikas, should collect larger forage in order to maximize energy/effort ratios. Recent evidence, however, did not support this hypothesis (Dearing, 1996; Gliwicz et al., 2006).

In this study, we compared the winter diets of collared pikas (*O. collaris*) to the available vegetation within their territories and experimentally tested the importance of forage size for winter diet selection. Specifically, we predicted that leaf size would influence forage selection, consistent with the plant morphology hypothesis.

Methods

STUDY AREA

The study was conducted in a 4 km² valley in the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13′N, 138°16′W). Vegetation cover was primarily lichen-heath, willow (*Salix* spp.), *Carex* spp., *Dryas octopetala*, and *Cassiope tetragona*. The alpine meadow was fragmented by large (up to 4 ha) boulder fields. Collared pikas, hoary marmots (*Marmota caligata*) and

arctic ground squirrels (*Spermophilus parryii plesius*) were the dominant mammalian herbivores.

STUDY SPECIES

Both the collared pika and the closely related American pika (*O. princeps*) inhabit alpine regions of western North America (Broadbooks, 1965; Smith et al., 1990) and are thought to be similar in most respects (Franken, 2002). Collared pikas are small (~160 g) central-place foragers that inhabit boulder fields in alpine and subalpine regions of Alaska, Yukon, western Northwest Territories, and northern British Columbia (Broadbooks, 1965; Smith et al., 1990). Pikas are behaviorally limited to foraging in meadows near the talus edge and create a strong gradient of decreasing grazing intensity outward from talus into adjacent meadows (Huntly et al., 1986; McIntire and Hik, 2005).

Pikas are an excellent model species for studying foraging behavior. They are easily live-trapped and marked with unique colored ear tags for later identification. They inhabit territories that are usually <50 m in diameter (Franken, 2002) and aggressively defend these territories against conspecifics (Conner, 1983; Smith and Ivins, 1986). They are insatiable hoarders of vegetation (McKechnie et al., 1994) and quickly discover and cache vegetation experimentally placed in their territories (Morrison et al., 2004; Koh and Hik, 2007). Caches in the rock matrix are sufficiently accessible to permit examination of stored material.

Rock-dwelling pikas, including the collared pika, forage for both summer and winter diets from the standing summer vegetation. Pikas consume summer forage immediately but harvest, transport, and store forage in caches (hay piles) for winter consumption (Dearing, 1997a). Haying contributes to winter survival and the successful initiation of reproduction in early spring (Smith and Ivins, 1986; Morrison, 2007). In some years, the date when haying behavior is first initiated also affects winter survival, and hay piles at our site appear to be of sufficient size to sustain pikas for the entire winter period (Morrison, 2007). Adults begin haying by mid-July and continue until snow cover reduces accessibility (K. O'Donovan, unpublished observations). Vegetation biomass peaks at the end of July and senescence begins in early August (McIntire and Hik, 2005). Haying activity peaks during this period (Morrison, 2007).

VEGETATION AVAILABILITY AND HAY PILE COMPOSITION

Across all years, experimental work was conducted between late July and early August to coincide with the peaks in vegetation biomass and haying activity in order to minimize seasonality effects on vegetation and pika behavior.

During late July–early August 2006, we estimated the percent cover of vegetation (i.e., excluding rock and soil) using 1 m × 1 m quadrats. All plant nomenclature followed Cody (2000). Five transects, placed in meadows 1–3 m from the talus edge, were used to estimate forage availability within each pika territory. Quadrats were representatively (i.e. non-systematically) placed in areas of observed foraging. Visual observations of haying, evidence of grazed plants, productivity (included lush, stunted, and sparse meadows) and distance from hay piles were used to select transects. Areas containing vegetation that pikas do not use (e.g., very tall deciduous shrubs) were not sampled. Pikas at our study site often inhabit inferior territories, typically containing areas of non-use, potentially because of interference and exploitative competition with hoary marmots for more productive sites (Franken, 2002).

The study followed Design III as classified by Thomas and Taylor (1990) and used sample protocol "A," defined by Manly et al. (2002). Following these classifications, use and availability were measured separately for each individual (Design III). Availability was defined as the percent cover per territory, and use was defined as species wet weight per hay pile (sample protocol "A"). Our definitions of availability, abundance, preference, and selectivity followed Johnson's (1980). *Availability* was the quantity of a resource accessible to an individual. It differed from *abundance*, which was the quantity in the environment, independent of the individual. *Preference* was the likelihood of being chosen if offered on an equal basis with other resources. *Selectivity* was measured by comparing use to availability. Usage disproportional to availability was said to be *selective*.

Vegetation samples were collected from active hay piles over five summers. Portions of some caches were buried deep in the rock matrix and were not sampled. Between 2002 through 2005, three small (<10 g) vegetation samples were collected from >75% of active hay piles in late July–early August. Each sample was collected from a different location within the hay pile and stored individually. Vascular plants were identified by species to determine hay pile compositions. Lichens and bryophytes were excluded from this analysis, but generally represented <5% of hay pile biomass. In late July–early August 2006, we randomly collected large 20 g (wet weight) samples from 24 territories within the study area. Hay pile samples were sorted, identified by species to determine composition, and then returned to the hay pile. Graminoids were classified as either sedges or grasses. Although pikas have characteristic harvest methods for each plant life form (e.g. forbs, evergreen shrubs, graminoids, etc.) (Huntly et al., 1986), intra-specific differences in plant morphology made sampling by weight (and not leaf counts) the most effective means of determining hay pile composition. This sampling method included portions of plants not consumed by pikas such as flower stems.

FORAGE PREFERENCE TRIALS

Forage preferences of haying pikas were determined using three cafeteria-style experiments, similar to those described by Morrison et al. (2004) and Koh and Hik (2007). Each cafeteria was constructed of adjacent polyvinyl chloride (PVC) tubes (diameter 10 cm, length 15 cm) that were capped at one end and laid on their side. For each trial, 10 ± 0.1 g of freshly cut forage were randomly allocated to the tubes. One treatment was allocated to each tube. Only leaves were presented (i.e. no stems, flowers, or seed heads).

Trials commenced when pikas began collecting vegetation from the tubes and were conducted for 1 hr of observed surface activity. Observations were stopped whenever pikas went belowground for longer than one minute (e.g., after detecting a predator). Only one trial was conducted for each pika. Once the target pika began to remove vegetation from the cafeteria (i.e. haying), cumulative selection (% removed) for each tube was recorded at 1-minute intervals for the duration of the trial. Morrison et al. (2004) found that >99% of all removed vegetation was due to haying activity rather than consumption.

In late July–early August 2004, we conducted manipulated leaf size trials. In the first experiment, we presented individuals with stalks of *Artemesia norvegica* (a forb) cut to 2, 5, and 10 cm lengths. In the second experiment, we presented 2 and 5 cm cut leaves of both *Carex consimilis* (a sedge) and *Polygonum bistorta* (a forb). *P. bistorta* leaves were trimmed to match the width of *C. consimilis* leaves (about 0.6 cm). *P. bistorta* is preferred to *C. consimilis* (Morrison et al., 2004). This experiment used a factorial design to assess the influence of both leaf size and species. We used these three species because we could manipulate their lengths and standardize their widths, they were relatively common in hay piles, and they were preferred to other plants in a previous study (Morrison et al., 2004).

In late July–early August 2006, we presented individual pikas with unmanipulated leaves. Forage species were selected based on their abundances in hay piles and included (ordered along a gradient of decreasing leaf size) *C. consimilis*, *Salix arctica* (a deciduous shrub), *S. reticulata* (a deciduous shrub), *S. polaris* (a deciduous shrub), and *Dryas octopetala* (a semi-evergreen shrub). One trial that we included in the analysis was terminated early after only 38 minutes when a neighboring pika began removing vegetation from the cafeteria.

NUTRIENT ANALYSIS

In early August 2006, we collected approximately 300 g (wet weight) of the five species used in the 2006 experiment for nutrient analysis. Samples were weighed and air-dried in the field and oven-dried upon return to the lab. Dried samples were analyzed for percent nitrogen (N) using Dumas dry combustion on a Carlo-Erba 1500 NC analyzer (Strada Rivol Tana, Milan, Italy).

SELECTION ANALYSES

We grouped vegetation into five plant life forms: (1) graminoids (grasses and sedges), (2) deciduous shrubs (*Salix* spp. and *Vaccinium* spp.), (3) semi-evergreen shrubs (*D. octopetala*), (4) forbs, and (5) other (lichens, mosses, and evergreen shrubs such as *C. tetragona*) based on pika harvesting methods. Pikas exhibited common collecting, transporting, and storing techniques for each life form. The "other" group consisted of forage species that have been consistently avoided by pikas in previous foraging studies (Gliwicz et al., 2006). We used compositional analysis to test for forage selectivity (Aebischer et al., 1993). Zero values were replaced by 0.05%, an order of magnitude less than the smallest recorded nonzero percentage (Aebischer et al., 1993). To conduct our analyses, we used the
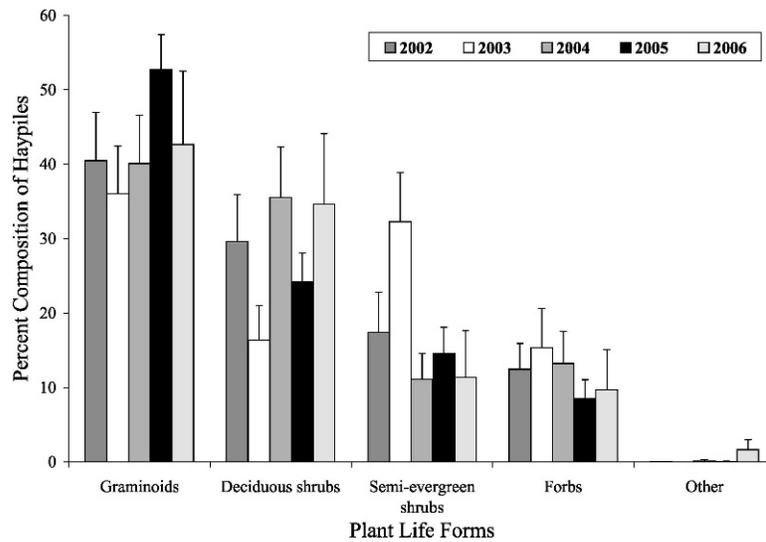
FIGURE 1. Composition (by weight) of collared pika hay piles from 2002 to 2006 ($n = 58, 60, 75, 151, 24$ hay piles) in southwest Yukon. Error bars represent 95% confidence intervals. The "other" category includes lichens, mosses, and evergreen shrubs. Between 2002 and 2005, lichens and bryophytes were excluded from analyses so the "other" category only includes evergreen shrubs in those years.

software R (Version 2.1.1; R Development Core Team, 2005) and the 'adehabitat' package (Version 1.5; Calenge, 2006).

Preferences were calculated using Rodgers' Index (Krebs, 1999). We developed general linear mixed-effects models (GLMM) in which leaf size (experiments 1 and 2) and species (experiments 2 and 3) were fixed factors and trial was a random factor. Because only one pika removed vegetation during any given trial, this was equivalent to blocking by individual pika.

Pikas are classical multiple prey loaders (Stephens and Krebs, 1986) because they transport multiple items during each haying trip. They carry vegetation crosswise and it extends out from both sides of their mouths. In the third experiment, we used load size (grams harvested per trip) as a surrogate for leaf size (grams per leaf). Load size was estimated as the forage removed (grams) during the first trip to each tube during the 2006 trials.

Results

Twenty-four adult pikas (12 female, 11 male, 1 unknown sex) were included in the selectivity study and were randomly selected from approximately 45 marked adult pikas at our study site in 2006. Our sample represents 53% (24/45) of the adult population. We pooled all adult age-classes and excluded juvenile pikas based on potential differences in selection criteria (Gliwicz et al., 2006). Males and females were pooled in our analyses following Morrison et al. (2004), who found no gender-specific differences.

Species used in the preference experiments were relatively common in hay piles. We conducted 12 trials in the first experiment, 19 in the second, and 24 in the third. The five plant species used in the third (2006) experiment constituted 66.9% $\pm$ 3.7 (95% confidence interval) of hay pile composition. The remaining thirds were comprised of species that were highly variable in abundance and occurrence, and site-specific. Hay piles contained an average of 7.3 $\pm$ 0.7 (95% CI) vascular plant species. Overall, 26 species were present in hay piles, with the dominant life forms being deciduous shrubs and graminoids (Fig. 1). We classified graminoids into two groups (grasses and sedges), and therefore the total number of species was underestimated. Forb biomass was predominantly vegetative as flowers of only four genera were collected (together, material from these four genera constituted less than 4% of mean hay pile composition). Flower stems, which were not usually consumed, were rare.

SELECTION ANALYSES

Collared pikas were selective (Aebischer's compositional analysis, $\Lambda = 0.156$, $P = 0.002$; Fig. 2) and selected in the following manner (from most to least preferred): deciduous shrubs = graminoids > semi-evergreen shrubs = forbs > other.
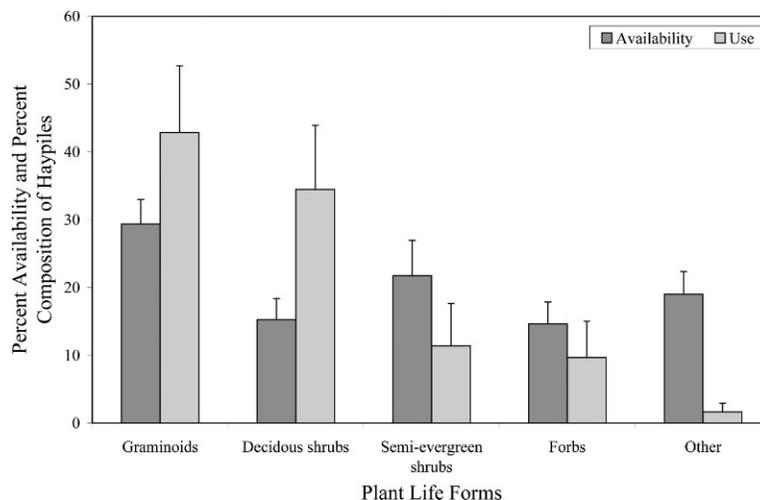

FIGURE 2. Forage selection by 24 collared pikas during summer 2006 summarized by plant life form. *Availability* was the percent cover per territory and *Use* was the percent composition (wet weight) of hay piles. Error bars represent 95% confidence intervals.
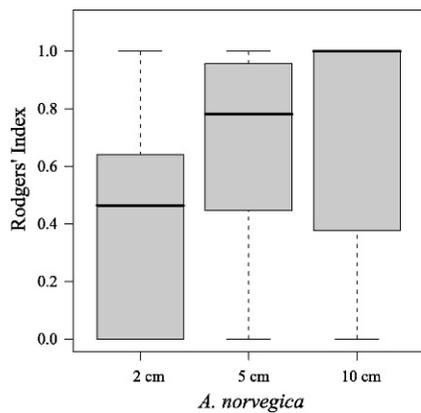
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FIGURE 3. Box and whisker plot of collared pika preferences for *Artemesia norvegica* leaves cut to 2, 5, and 10 cm lengths from 12 trials in the second cafeteria-style preference experiment. Preference scores are arcsine transformed Rodgers' Index values. Dark horizontal lines represent the medians, boxes represent the 25–75th percentiles, and whiskers represent 10–90th percentiles.

FIGURE 4. Box and whisker plot of collared pika preferences for *Carex consimilis* and *Polygonum bistorta* leaves cut to 2 and 5 cm lengths from 19 trials in the third cafeteria-style preference experiment. Preference scores represented are arcsine transformed Rodgers' Index values. Dark horizontal lines represent the medians, boxes represent the 25–75th percentiles, and whiskers represent 10–90th percentiles.

In the first leaf manipulation experiment, pikas tended to prefer larger leaves (10 and 5 cm lengths) to shorter leaves (2 cm) (GLMM, $F = 2.90$, $P = 0.076$, d.f. $= 22$; Fig. 3). Pikas selected 5 cm leaves over 2 cm leaves (GLMM, $F = 11.61$, $P = 0.001$, d.f. $= 54$; Fig. 4) and selected *P. bistorta* leaves over *C. consimilis* leaves in the second experiment (GLMM, $F = 8.19$, $P = 0.006$, d.f. $= 54$). There was no leaf size × species interaction ($F = 0.56$, $P = 0.455$, d.f. $= 54$).

In the third (2006) experiment, collared pikas exhibited the following preference groupings (from most to least preferred): (1) *C. consimilis;* (2) *S. arctica, S. reticulata, S. polaris*; and (3) *S. reticulata, S. polaris, D. octopetala* (GLMM, $F = 18.61$, $P = 0.001$, d.f. $= 115$; Fig. 5). That is, *C. consimilis* was more highly selected than any other species, and the *Salix* species were selected equally. However, selections of *S. reticulata* and *S. polaris* (but not *S. arctica*) were similar to *D. octopetala*.

Discussion

Leaf size influenced forage selection in the preference trials. Pikas appeared to prefer large leaves compared to medium leaves, and medium leaves to small leaves (experiment 1). Pikas also preferred larger leaves to smaller leaves, but inter-specific differences also influenced preferences (experiment 2). In the third experiment, species rank order was related to leaf size such that the largest leaves (*C. consimilis*) were most preferred and the smallest leaves (*D. octopetala*) were least preferred. Preference for larger leaves with relatively high energy/effort ratios agrees with the predictions of an optimal foraging strategy (Stephens and Krebs, 1986).

Similar results were observed in our use:availability analysis, which indicated that deciduous shrubs and graminoids were most highly selected by pikas, followed by semi-evergreen shrubs and forbs. Evergreen shrubs, mosses, and lichens were least selected. This order closely followed leaf size, with pikas showing preference for plants with larger leaves.

Our results provide strong support for the plant morphology hypothesis which posits that central-place foragers should collect larger species to maximize the amount of vegetation collected per foraging trip (Huntly et al., 1986). These results contrast with other studies of rock-dwelling pikas where other factors appeared to have a larger influence on forage selection (Dearing, 1996; Gliwicz et al., 2006). For example, Dearing (1996) suggested that
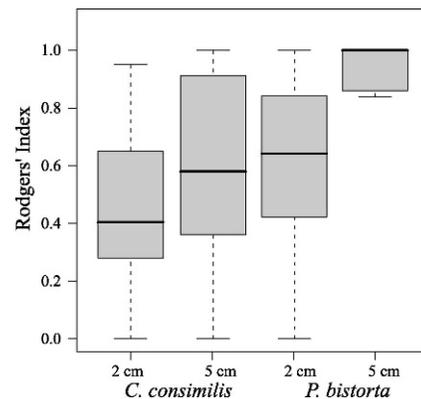
the plant morphology hypothesis was weak because pikas did not collect cushion plants that had been experimentally harvested. Instead, we suggest that pikas may instinctively avoid collecting vegetation such as cushion plants, evergreen shrubs, and lichens that remain accessible during the winter and early spring (Millar and Zwickel, 1972; Conner, 1983).

Rock-dwelling pikas are generalists and consume winter diets that appear to vary between sites. *O. princeps* diets are dominated by forbs in Colorado, U.S.A. (Huntly et al., 1986; Dearing, 1996), and by graminoids and deciduous shrubs in Alberta, Canada (Millar and Zwickel, 1972). At our Yukon site, *O. collaris* consumed mostly graminoids and deciduous shrubs. In Eastern Siberia, variability in *O. hyperborea* diets was attributed to local differences in vegetation types (Gliwicz et al., 2006). Collectively, these reports suggest that the relative importance of pika forage selection criteria is likely site-dependent.

Plant chemical defenses have also been identified as a critical factor influencing forage selection at some sites (Dearing, 1996; Gliwicz et al., 2006). In Colorado, *O. princeps* collect *Acomastylis rossii*, a strongly defended forb, which becomes more palatable after storage (Dearing, 1996, 1997b). The species comprises 60–77% of the winter diet and 91–96% of the total phenolics. In our study, we did not quantify the toxicity of forage species because chemical defenses did not appear to drive forage selection and so there were no obvious candidate species or defenses. Instead, pikas selected a variety of species, all potentially defended by secondary compounds. For example, deciduous shrubs containing tannins were collected, while tannin-rich evergreen shrubs were not. Similarly, graminoids were selected over forbs. In separate cafeteria-style preference experiments (Koh and Hik, 2007), pikas actively avoided collecting *Festuca altaica* infected with endophytes. Overall, these results suggest that pikas at our site did not prefer plants rich in secondary compounds that would become more palatable after storage; however, further research that tests the actual palatability and toxicity of vegetation at our site is required.

In conclusion, our evidence indicates that pikas appear to maximize their energy/effort ratios when foraging for their winter diet by selecting large-leafed plants. By selecting large-leafed plants, pikas can transport more vegetation per trip and accumulate larger hay piles during the limited haying period. This energetically efficient foraging strategy is central to surviving seasonal food scarcity.
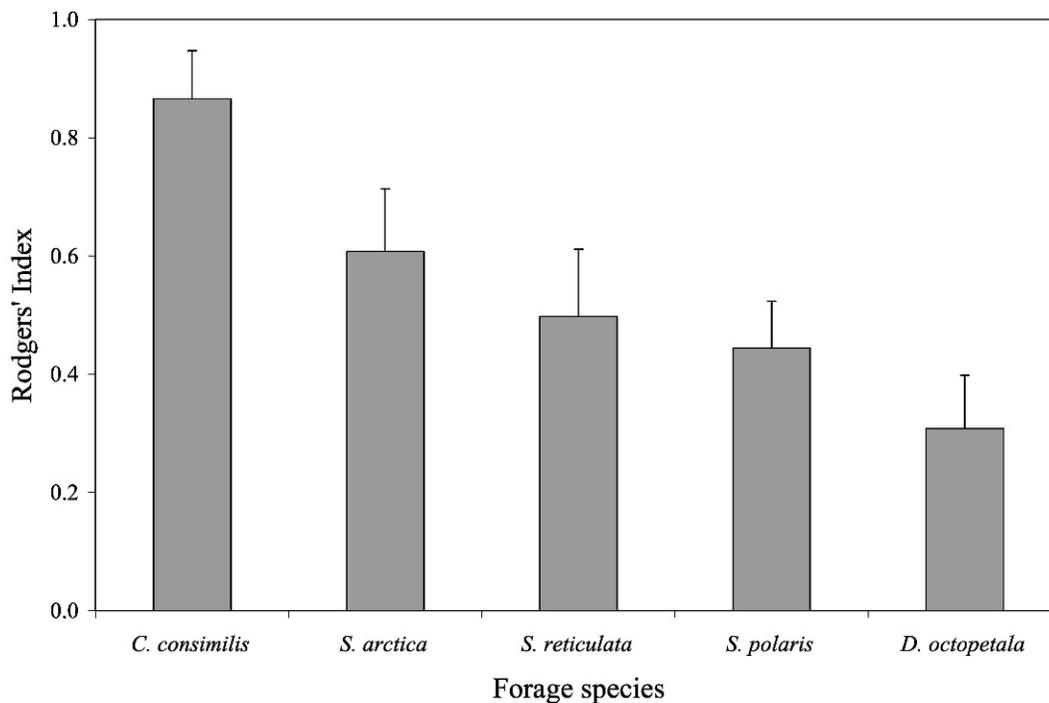
	C. consimilis	S. arctica	S. reticulata	S. polaris	D. octopetala
Load Size	1 (2.04)	2 (1.34)	2 (1.34)	3 (1.20)	4 (1.13)
Crude Protein	1 (25.3)	4 (15.8)	3 (17.6)	5 (11.8)	2 (20.6)
Water Content	4 (0.69)	3 (0.70)	2 (0.72)	1 (0.73)	5 (0.63)
Availability	2 (15.8)	5 (0.9)	4 (2.8)	3 (7.2)	1 (21.7)

FIGURE 5. Forage preferences (mean $\pm$ 95% CI for arcsine transformed Rodgers' Index scores) stratified by species of 24 collared pikas in the southwest Yukon in late July and early August 2006. Morphological, nutritional, and environmental data are presented as rank order of the amount for each species. Actual values are provided in parentheses. *Load Size* was grams harvested per trip; *Crude Protein* was % CP = nitrogen $\times$ 100/16 (Robbins, 1983); *Water Content* was wet weight:dry weight ratio; *Availability* was mean percent cover in pika territories.

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