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Author(s): Mark A. Edwards, Andrew E. Derocher, Keith A. Hobson, Marsha Branigan and John A. Nagy

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Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic

Mark A. Edwards · Andrew E. Derocher ·
Keith A. Hobson · Marsha Branigan ·
John A. Nagy

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Abstract Categorizing animal populations by diet can mask important intrapopulation variation, which is crucial to understanding a species' trophic niche width. To test hypotheses related to intrapopulation variation in foraging or the presence of diet specialization, we conducted stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) on hair and claw samples from 51 grizzly bears (*Ursus arctos*) collected from 2003 to 2006 in the Mackenzie Delta region of the Canadian Arctic. We examined within-population differences in the foraging patterns of males and females and the relationship between trophic position (derived from $\delta^{15}\text{N}$ measurements) and individual movement. The range of $\delta^{15}\text{N}$ values in hair and claw (2.0–11.0‰) suggested a wide niche width and cluster analyses indicated the presence of three

foraging groups within the population, ranging from near-complete herbivory to near-complete carnivory. We found no linear relationship between home range size and trophic position when the data were continuous or when grouped by foraging behavior. However, the movement rate of females increased linearly with trophic position. We used multisource dual-isotope mixing models to determine the relative contributions of seven prey sources within each foraging group for both males and females. The mean bear dietary endpoint across all foraging groups for each sex fell toward the center of the mixing polygon, which suggested relatively well-mixed diets. The primary dietary difference across foraging groups was the proportional contribution of herbaceous foods, which decreased for both males and females from 42–76 to 0–27% and 62–81 to 0–44%, respectively. Grizzlies of the Mackenzie Delta live in extremely harsh conditions and identifying within-population diet specialization has improved our understanding of varying habitat requirements within the population.

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M. A. Edwards (✉) · A. E. Derocher · J. A. Nagy
Department of Biological Sciences,
University of Alberta, Edmonton, AB T6G 2E9, Canada
e-mail: mark.edwards@gov.ab.ca

K. A. Hobson
Environment Canada, 11 Innovation Building,
Saskatoon, SK S7N 3H5, Canada

K. A. Hobson
Department of Biology, University of Saskatchewan,
Saskatoon, SK S7N 5E2, Canada

M. Branigan
Department of Environment and Natural Resources,
Government of Northwest Territories,
Inuvik, NT X0E 0T0, Canada

Present Address:

M. A. Edwards
Mammalogy, Royal Alberta Museum,
Edmonton, AB T5N 0M6, Canada

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Introduction

Ecologists have frequently assigned species to broad dietary categories and have not emphasized variation within populations in favor of identifying a species' typical foraging behavior (Urton and Hobson 2005; Loudon et al. 2007; Newsome et al. 2009). Recent papers highlight the significance of intrapopulation variation in foraging behavior and the need to understand such variability (Ben-David et al. 1997; Bolnick et al. 2003). Diversity in resource use or diet specialization can result in differences in individual fitness

with ecological, evolutionary and conservation implications (Bolnick et al. 2003; Svanback and Bolnick 2007). Therefore, understanding how dietary patterns within populations are aggregated by similarities among individuals is integral to conceptualizing processes in food web dynamics (Tinker et al. 2008; Newsome et al. 2009).

Within Carnivora, food habits range from carnivory to herbivory (Macdonald 1979). Carnivores with a higher proportion of meat in their diet generally occur at higher latitudes (Vulla et al. 2009), and range farther than carnivores specializing on insects, vegetation or fruits (Gittleman and Harvey 1982; Mace et al. 1983). Animals with more meat in their diet move faster as they search for low-density and/or vagile prey, whereas animals with a predominantly herbaceous diet move slower through habitats as they forage on more evenly distributed and less mobile or immobile prey (Gittleman and Harvey 1982; Mace et al. 1983). Omnivory, broadly defined as feeding across multiple trophic levels, was previously thought to promote instability within food webs, but omnivory was more recently proposed to stabilize a food web through interactions with habitat, community composition, and energy flow (Pimm and Lawton 1978; Pimm et al. 1991; Morris 2005). Because of their ecological plasticity, omnivores may occupy different trophic positions depending on the ecological attributes of the occupied area, operating as a carnivore in one and as a herbivore in another (Stenroth et al. 2008). Omnivores do not have an easily defined position in food webs, and their ecological role has not received the same attention afforded to obligate herbivores and carnivores, which have well-defined trophic positions (Pimm et al. 1991). To better understand the role of omnivores in ecosystems, the importances of different components of their diet should be established (Tillberg and Breed 2004).

Analysis of naturally occurring stable isotope ratios has been used across diverse faunal assemblages to better delineate the dietary contributions of different foods (Peterson and Fry 1987; Newsome et al. 2007). Stable isotope analysis can increase our understanding of food web structure and the proportional contributions of different dietary groups and their relative nutritional values to consumers (Deniro and Epstein 1978; Hobson 1999). An advantage of using stable isotope analysis to determine diet is that it reflects assimilated foods and not simply ingested foods (Peterson and Fry 1987). Stable carbon isotope analysis can reveal important information on assimilated foods, and provides a method of inferring the use of terrestrial versus marine prey (Peterson and Fry 1987). Isotopic differences among foods within an ecosystem result in a stepwise trophic enrichment in stable isotope values of nitrogen ($\delta^{15}\text{N}$) by approximately 2–5‰ (Deniro and Epstein 1978, 1981).

We used stable isotope analysis to test hypotheses related to trophic position for a large Arctic omnivore, the

barren ground grizzly bear (*Ursus arctos*) of the Mackenzie Delta region. Grizzly bears in the Canadian Arctic have larger home ranges than more southern populations (Nagy and Haroldson 1990) and exhibit low site fidelity and interannual home range drift (Edwards et al. 2009). Grizzly bears are sexually dimorphic: males are larger than females and generally have both higher protein diets (Hilderbrand et al. 1999) and larger home ranges (Dahle and Swenson 2003). Bears are characterized by their evolutionary and ecological plasticity and exploit a wide variety of diets, habitats, and geographical ranges (Stirling and Derocher 1990). Interpopulation variation in the diet of grizzlies has been noted, with some populations along the Pacific coast of North America being primarily piscivorous (Ben-David et al. 1998; Mowat and Heard 2006), whereas for other populations, >90% of their diet consists of berries, forbs, grasses, and sedges, even when animal protein is abundant (Rode et al. 2001). The wide ecological niche, therefore, presents the grizzly bear as a suitable subject for examining intrapopulation variation in foraging behavior.

The niche variation hypothesis proposes that interindividual variation in foraging behavior is the driver for niche width (Van Valen 1965). For grizzly bears, a pertinent question is whether a population is composed of generalists exploiting a diverse diet or whether it is composed of specialists focusing on fewer species (Van Valen 1965; Grant et al. 1976). Competition among conspecifics can result in individual diet specialization within populations of ecologically heterogeneous individuals (Bolnick et al. 2003; Svanback and Bolnick 2007). Although bears are opportunistic and their diet is generally omnivorous, we tested the hypothesis that different foraging behaviors exist for male and female grizzlies within a population using stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) for two metabolically inert tissues. To test the hypothesis that higher trophic position requires increased foraging effort, we examined the trophic niche width of grizzly bears and metrics of their range use, including home range size and movement rate. We predicted that bear trophic position would be positively correlated with these range-use metrics.

Materials and methods

Study area

The study was conducted near the northern edge of the grizzly bear's North American distribution in Canada's western Arctic, south of the Beaufort Sea and encompassing approximately 23,000 km² (Fig. 1). The region is characterized by long, cold winters and short, cool summers (Black and Fehr 2002). The area can remain snow-covered

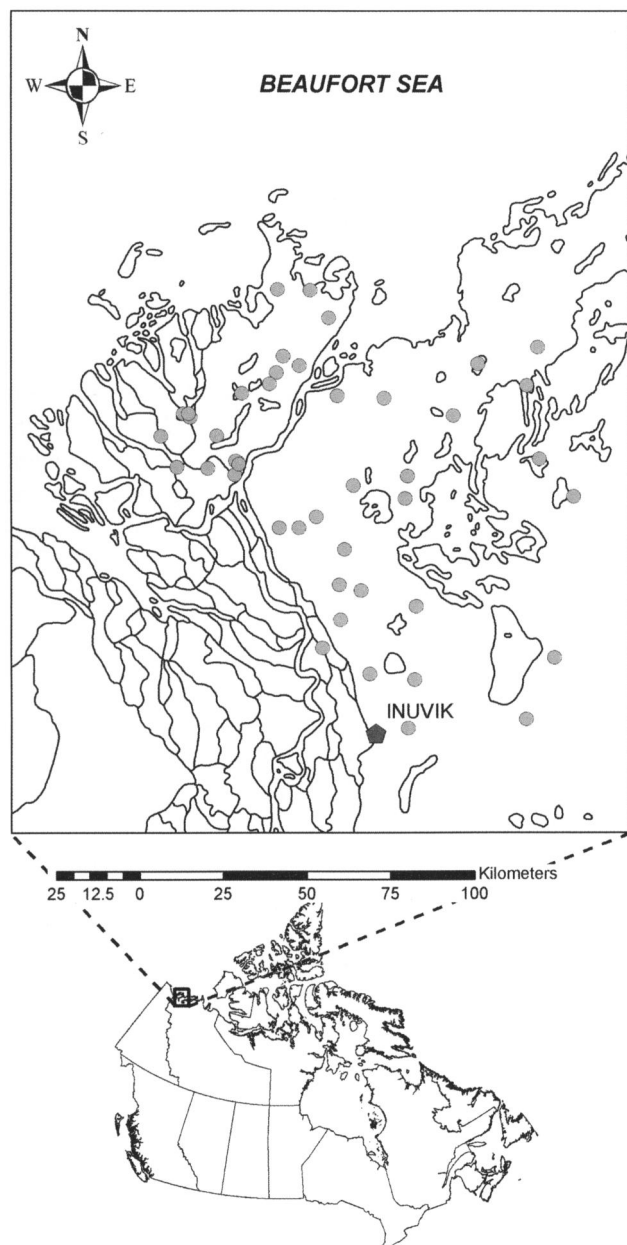


Fig. 1 Map of the Mackenzie Delta study area in the Northwest Territories, Canada, showing the distribution of sampled grizzly bears (2003–2006) by capture location (gray circles)

from mid-October to mid-May, and the vegetation growing season is short (Nagy et al. 1983; Black and Fehr 2002). Dominant geographical features include numerous lakes and rivers, the Mackenzie Delta, and environmental conditions that transition south to north from boreal forest dominated by spruce (*Picea glauca* and *P. mariana*), to open tundra with scattered trees and shrubs, to coastal habitat (MacKay 1963).

From grizzly bear scat analysis (Nagy et al. 1983), herbaceous foods in the Mackenzie Delta region include crowberry (*Empetrum nigrum*), buffaloberry (*Shepherdia*

canadensis), bearberry (*Arctostaphylos* spp.), alpine blueberry (*Vaccinium uliginosum*), and lingonberry (*V. vitis-idaea*), which occur throughout the region (Porsild and Cody 1980). Other common herbaceous foods include sweetvetch (*Hedysarum alpinum*), horsetail (*Equisetum* spp.), grasses and sedges (*Carex* spp.) (Porsild and Cody 1980). Although herbaceous food sources are widely distributed, productivity is generally low and varies annually (Chapin and Shaver 1985; Shevtsova et al. 1995). Mammalian prey species include barren-ground caribou (*Rangifer tarandus groenlandicus*), semi-domesticated reindeer (*R. t. tarandus*), moose (*Alces alces*), brown lemmings (*Lemmus sibiricus*), collared lemmings (*Dicrostonyx torquatus*), Arctic ground squirrels (*Spermophilus parryi*), muskrat (*Ondatra zibethicus*), beaver (*Castor canadensis*), and microtines (Nagy et al. 1983). The Beaufort Sea provides ringed seals (*Pusa hispida*), belugas (*Delphinapterus leucas*), and Arctic char (*Salvelinus alpinus*). Snow geese (*Chen caerulescens*) nest in the area. Broad whitefish (*Coregonus nasus*) are found in the lakes, rivers, and streams and are prey for grizzlies (Barker and Derocher 2009).

Sample collection

Grizzly bears were captured in May 2003–2006, shortly after they emerged from overwinter dens. Bears were immobilized by remote injection of Telazol® (Ayerst Laboratories Inc., Montreal, QC, Canada) (Woodbury 1996). Sampling was biased toward females to minimize interference with hunting of males by nearby communities. Bears were fitted with global positioning system (GPS) telemetry collars (Telonics Inc., Mesa, AZ, USA) linked to Argos satellites (CLS America Inc., Largo, MD, USA). Collars were programmed to acquire a location once every 4 h from 1 April to 30 November during the non-denning season and then shut off to prolong battery life. Each collar had a programmable release mechanism (Telonics Inc.). Bears were marked with numbered plastic ear tags and lip tattoos for subsequent identification. From each captured bear, we plucked forearm hair, so that the full shaft from root to tip was sampled, and collected from the forepaw a longitudinal sample of the claw unguis from matrix to tip using a vegetable peeler. Handling time for each bear was under 60 min.

Range use

GPS telemetry locations were imported into a geographic information system (ArcView 3.2 or 9.2, Environmental Systems Research Institute, Redlands, CA, USA) to quantify range-use metrics for each collared bear. We used the Animal Movement extension (Hooge and Eichenlaub 1997) to estimate the 95% annual home range using the

fixed kernel technique and least-squares cross-validation for bandwidth selection (Worton 1989; Seaman and Powell 1996). Hawth's Analysis Tools for GIS 1.1 (Beyer 2005) was used to determine the mean movement rate in meters per hour (m/h).

Stable isotope analysis

Stable isotope analysis was conducted on hair and claw samples and on potential food sources, including plant and animal prey types (Fig. 2). Hair and claw tissue represent an archive of dietary composition during the last growth period (Peterson and Fry 1987), which for bears is the previous active season from April to November. Grizzly bears molt once a year between June and July, and hairs collected before the molt represent the feeding history for the preceding active season (Jacoby et al. 1999; Hobson et al. 2000). Hair growth starts in May and is nearly constant from the hair follicle for hairs collected from the same area on the body, and stops before hibernation in autumn (Mizukami et al. 2005). Claw growth is similar to hair, with growth starting from the claw base and continuing throughout the non-denning period, stopping during the quiescent phase (Belant et al. 2006).

All samples were cleaned with distilled water to remove debris. Hair and claw samples were washed three times in 2:1 methanol:chloroform solution for 10 mins each to remove surface oils and then allowed to dry before being freeze dried at -50°C for ≥ 24 h (Hilderbrand et al. 1996). Hair was then cut into small pieces and claw was ground using a mortar and pestle. Hair and claw samples were powdered using a cryogenic mill (Retsch Inc., Newtown, PA, USA). We milled samples twice to maximize

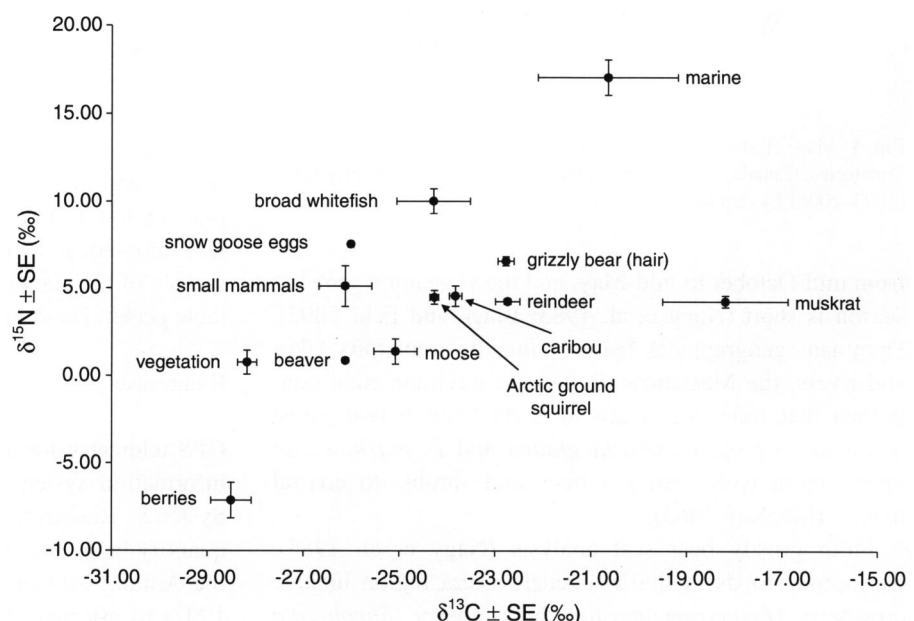
homogenization of the samples. Plant and animal prey tissue samples were cut into small pieces and freeze dried at -50°C for ≥ 24 h. Animal tissue samples were soaked in 2:1 methanol:chloroform solution for 24 h, rinsed and decanted twice to remove lipids, and air dried before powdering by mortar and pestle.

Subsamples of all material were analyzed for isotopic measurement using a Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS) interfaced with a Robo-Prep elemental analyzer at the Centre for Soil Research (Department of Soil Research, University of Saskatchewan, Saskatoon, SK, Canada). Results are reported as ratios in parts per thousand (‰) relative to the Vienna PeeDee Belemnite ($\delta^{13}\text{C}$) standard or atmospheric nitrogen ($\delta^{15}\text{N}$). Replicate analysis of (egg albumen and whale baleen) standards within runs yielded an estimate of analytical error of ± 0.1 and ± 0.3 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements, respectively.

Data analysis

We used Hotelling's T^2 analysis to determine if $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for hair and claw differed. Differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for hair and claw between male and female grizzly bears were then tested using a one-factor multivariate analysis of variance (MANOVA). Following the results of the MANOVA, we used STATA 10.0 (StataCorp LP, College Station, TX, USA) and PC-ORD 5.0 (McCune and Mefford 1999) statistical software to perform Ward's minimum variance cluster analysis using $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values derived from hair and claw (a four-variable model) to identify any distinct foraging groups for males and females separately. We used the resulting

Fig. 2 Distribution of mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) for grizzly bear hair and uncorrected values for plant and animal prey sampled in the Mackenzie Delta region, Northwest Territories, Canada



dendrograms and three diagnostic stopping tools to determine the optimal number of clusters that best fit the data. With the dendrogram, we examined linkage distances and Wishart's (1969) objective function distance, which is a measure of the loss of information as bears are added to groups. Next, we estimated the Duda and Hart index, the pseudo t^2 statistic (Duda and Hart 1973; Rabe-Hesketh and Everitt 2004), and the Calinski and Harabasz pseudo F -statistic (Calinski and Harabasz 1974). Only hair samples were used in subsequent analyses because the hair provided a complete archive of the bear's diet during the previous active season from the last molt.

Linear regression and Kruskal–Wallis analysis were used to examine the relationship between male or female trophic position (as indicated by $\delta^{15}\text{N}$ values) or foraging group and metrics of range use, including home range size or movement rate. We assumed a $\delta^{15}\text{N}$ trophic discrimination factor of 3.4‰ (Urton and Hobson 2005).

Food sources with distinctive isotopic values were used in mixing models to determine their relative contributions to male and female grizzly bear diets. We used Isosource (Phillips and Gregg 2003), which is a probabilistic model that identifies a range of possible dietary inputs when the number of sources exceeds $n + 1$ isotopes for up to ten sources. As suggested by Phillips et al. (2005) we used the ecology of grizzly bear prey and their isotopic endpoints to a priori aggregate plant and animal prey into seven isotopically distinct food groups, including broad whitefish, snow goose eggs, muskrat, small mammals (brown lemmings, collared lemmings and microtines), aquatic browsers (beaver and moose), terrestrial mammals (caribou, reindeer and Arctic ground squirrel), and herbaceous foods (horsetail, grass, sedge, sweetvetch, and all berry species). Because of the proximity of the Beaufort Sea, there was potential for bears to exploit marine-based food sources such as ringed seal, beluga whale and Arctic char; however, movement patterns and range use of collared bears suggested that this possibility was small and that the contribution to the bears' diet was likely minimal. Therefore, to improve the interpretability of the mixing model, marine-based foods were omitted.

Isosource uses an iterative approach to consider all possible solutions to the measured mean isotopic value for the mixture and the mean values for the source endpoints (Phillips and Gregg 2003; Urton and Hobson 2005). Isosource requires information on diet-to-tissue discrimination, tolerance permitted around the model solution, and the interval increment used in the iterative procedure. We used a carbon diet–tissue discrimination correction factor of +2.6‰ as determined by Roth and Hobson (2000) for captive-raised red foxes (*Vulpes vulpes*). To account for variation in nitrogen isotopic discrimination due to diet quality, we used the linear function of Robbins et al. (2005);

$$y = 11.12 - 0.094x,$$

where x represents the protein quality for fish (92%), mammals and birds (78%), vegetation (71%), and berries (55%). The potential uncertainty of measurement error and the sample variability for sources and mixtures were incorporated into the model using a tolerance value of 0.1‰ and an interval increment of 1‰ (Phillips and Gregg 2003; Urton and Hobson 2005). Isosource is robust against outliers and variation in mass balance tolerance and interval increment (Phillips and Gregg 2003).

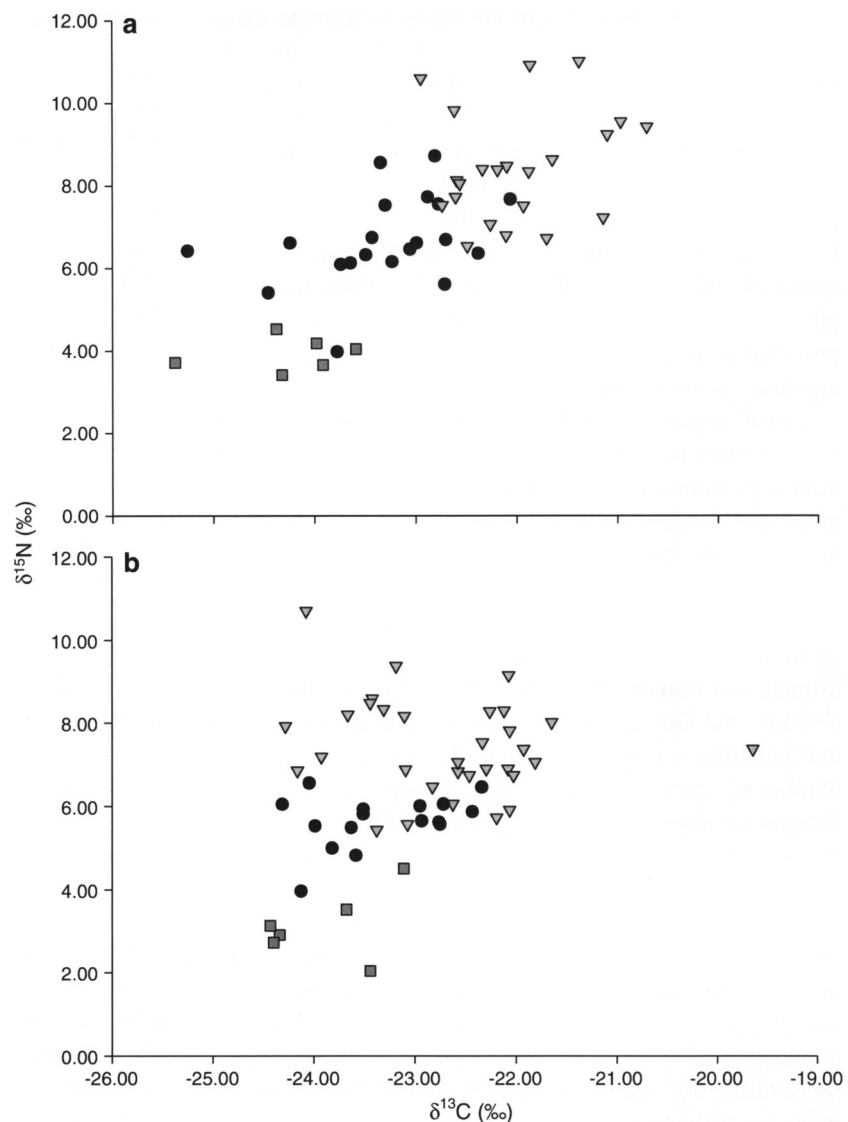
Results

Hair samples and claw shavings were obtained from 51 bears (Fig. 1). Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differed between grizzly bear hair and claw (Hotelling's T^2 , $F_{2,49} = 8.11$; $P < 0.01$). Although differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can be expected between certain tissues sampled from the same individual due to variation in diet–tissue fractionation, Hobson et al. (1996) demonstrated that there was no difference in the level of enrichment for hair and claw. However, unlike hair samples that included the entire shaft from root to tip, the base of the claw could not be sampled because it is under the skin in live bears and the tip is abraded through activity. Therefore, claw shavings represented a truncated record of the bear's diet during the previous non-denning period compared to sampled hair, which provided a complete record for the same period. The differences between hair and claw probably contributed to the different stable isotope values for these two metabolically similar tissues.

When values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for hair and claw were compared by sex, we found a significant difference for males ($n = 24$) and females ($n = 27$) (Wilks $\lambda = 0.76$; $F_{2,49} = 3.48$; $P = 0.01$). Therefore, examinations of within-population prey specialization, the relationship between trophic position and range use, and the proportional contributions of seven food sources to grizzly bear diet were considered independently by sex.

The range of values for $\delta^{15}\text{N}$ in hair and claw for both males and females suggested a wide niche width for the grizzly bears of the Mackenzie Delta region, crossing about three trophic levels (range 2.04–11.01‰; Fig. 3a, b). Ward's cluster analysis supported the observed wide niche width and suggested grouping at the level of three clusters for both male and female bears. For males, three clusters were supported by the larger values for the Duda and Hart index and the pseudo F -statistic, and a small pseudo t^2 statistic. For females, grouping at the level of three clusters was also supported by the larger value of the Duda and Hart index and the smaller pseudo t^2 statistic, however,

Fig. 3 Results of Ward's cluster analysis showing group membership of the three identified foraging groups 1 (gray squares), 2 (black circles), and 3 (gray triangles), delineated using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) from hair samples and claw shavings collected from **a** male and **b** female grizzly bears captured from 2003 to 2006 ($n = 51$) in the Mackenzie Delta region, Northwest Territories, Canada



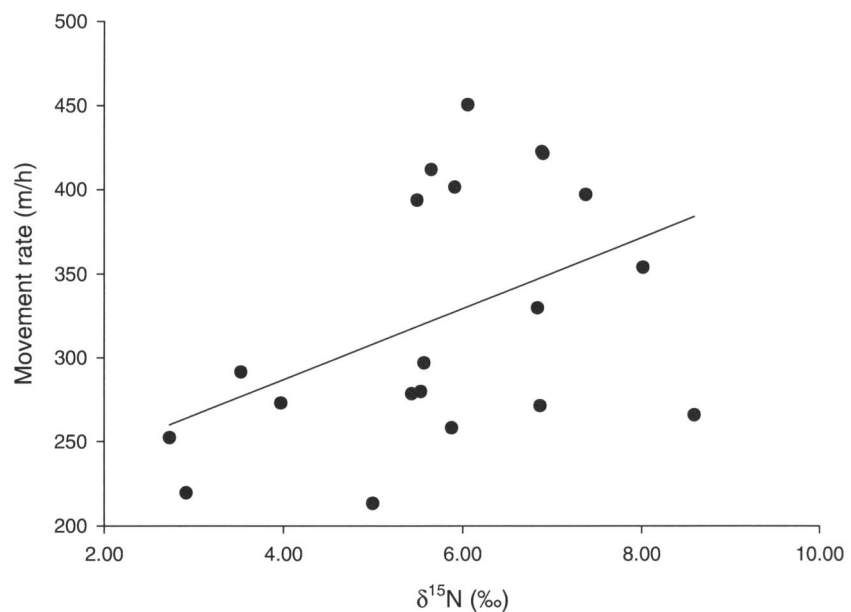
the pseudo F -statistic was inconclusive. To distinguish among the different groups we used their trophic position, with foraging group 1 as the lowest and 3 as the highest (Fig. 3a, b).

Of the 51 bears captured, 26 were fitted with GPS radiocollars and 14,924 locations were recorded. We found no (linear) relationship between $\delta^{15}\text{N}$ values from hair and annual home range size for males ($\bar{x} = 787 \text{ km}^2$, 95% confidence interval (CI) ± 262 ; $F_{1,4} = 4.45$; $P = 0.10$; $n = 6$) or females ($\bar{x} = 766 \text{ km}^2$; 95% CI ± 276 ; $F_{1,18} = 0.41$; $P = 0.53$; $n = 20$). These results were further corroborated by the Kruskal–Wallis test, which resulted in no significant effect of $\delta^{15}\text{N}$ on home range size when examined by foraging group for males ($X^2 = 3.57$; $df = 2$; $P = 0.17$) or females ($X^2 = 3.19$; $df = 2$; $P = 0.2$). Further, we found no significant relationship between $\delta^{15}\text{N}$ and the mean annual movement rate of males when examined by linear regression ($F_{1,4} = 5.44$;

$P = 0.08$), or by Kruskal–Wallis test on foraging group ($X^2 = 3.57$; $df = 2$; $P = 0.17$). In contrast, the mean movement rate of females increased with trophic position when examined by linear regression ($F_{1,18} = 4.41$; $P = 0.05$; $adj-R^2 = 0.15$) (Fig. 4). However, the Kruskal–Wallis test of $\delta^{15}\text{N}$, when examined by female foraging group, on mean annual movement rate was not significant ($X^2 = 5.13$; $df = 2$; $P = 0.08$).

Mixtures for both male and female grizzly bears fell toward the centers of their respective broad mixing polygons, indicating model convergence and consumption of all food types used in the mixing model by both sexes. There were, however, differences in the proportional contributions of the seven food sources among the three male and female foraging groups (Figs. 5, 6). The most prominent difference among all the foraging groups, irrespective of sex, was the proportion of herbaceous foods. For both males and females, there was a progressive decrease in the

Fig. 4 Relationship between trophic position or $\delta^{15}\text{N}$ (‰) and movement rate ($F_{1,24} = 6.53$; $P = 0.02$, $\text{Adj-}R^2 = 0.18$) of female grizzly bears monitored from 2003 to 2006 ($n = 20$) within the Mackenzie Delta region, Northwest Territories, Canada



importance of herbaceous foods from foraging group 1 to group 3. The biggest difference in the proportional contributions of the seven food sources between males and females occurred in foraging groups 1 and 3. More specifically, although the importance of herbaceous foods in the diet was similar for male and female foraging groups, the use of animal protein, whether terrestrial, avian or aquatic, was potentially higher for males in foraging groups 1 and 3 than for females.

For males in foraging group 1, herbaceous foods (1–99th percentile, 42–76%) contributed the majority of the bear's diet, with aquatic browsers forming a potentially important secondary food source (0–51%), and the other food sources likely contributing less to their diet. For foraging group 2, herbaceous foods contributed 8–56% and aquatic browsers and small mammals, 0–72 and 0–54%, respectively. Bears included in foraging group 3 assimilated the lowest proportions of herbaceous foods (0–27%); small mammals (0–82%) and terrestrial (0–66%) were potentially important primary food sources, followed by snow goose eggs (0–62%), and broad whitefish (0–61%). From foraging group 1 to 3, snow goose eggs contributed from 0–19 to 0–62%, small mammals from 0–28 to 0–82%, broad whitefish from 0–19 to 0–61%, and terrestrial from 0–31 to 0–66%.

Similar to males, herbaceous foods (62–81%) also contributed the majority of the diet for female bears in foraging group 1 with aquatic browsers as a potentially important secondary food source (0–30%). In addition, muskrat contributed 7–16% of the diet for females in foraging group 1. For foraging group 2, herbaceous foods contributed 6–59% and aquatic browsers 0–83%. Female bears in foraging group 3 consumed the lowest proportions of herbaceous foods (0–44%); aquatic browsers (0–73%)

and terrestrial (0–66%) were potentially important primary food sources, followed by small mammals (0–59%). From foraging groups 1–3, snow goose eggs contributed from 0–5 to 0–40%, and broad whitefish from 0–5 to 0–39%.

Discussion

Intrapopulation variation in the diet of grizzly bears in the Mackenzie Delta region supported our prediction that different foraging groups would be present in the population and that trophic position would be related to movement rate. Importantly, we found evidence that differences in the foraging behaviors were largely driven by the proportional use of herbaceous food types. We also found that the movement rate of females increased with trophic position, providing support for the idea that search effort increases with the level of carnivory. Because our analysis was conducted using hair and claw tissues, which have known temporal integration periods, and the study area presented a constant isotopic baseline, we were confident that the isotopic variation observed in grizzly tissues resulted from individual-level diet specialization among sampled bears.

Grizzly bears have a wide niche width across different populations (Hilderbrand et al. 1996; Mowat and Heard 2006); however, we found that even within populations, individual diets ranged across several trophic levels. We used a single diet–tissue discrimination value of +2.6‰ to predict bear diets from hair and claws, but this experimentally derived value was based on high-protein diets and not the omnivorous diet of wild grizzlies. However, a recent estimate for the $\delta^{13}\text{C}$ diet–tissue discrimination factor corresponding to a low-protein, herbivorous diet was

Fig. 5 Mixing polygon for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) of seven food sources (black triangles) for male grizzly bears sampled from 2003 to 2006 ($n = 24$) in the Mackenzie Delta region, Northwest Territories, Canada. Percentile ranges (1–99th percentile) show feasible contributions from each source to the mixture (black circles) for **a** the more herbivorous, **b** the omnivorous, and **c** the more carnivorous male bear

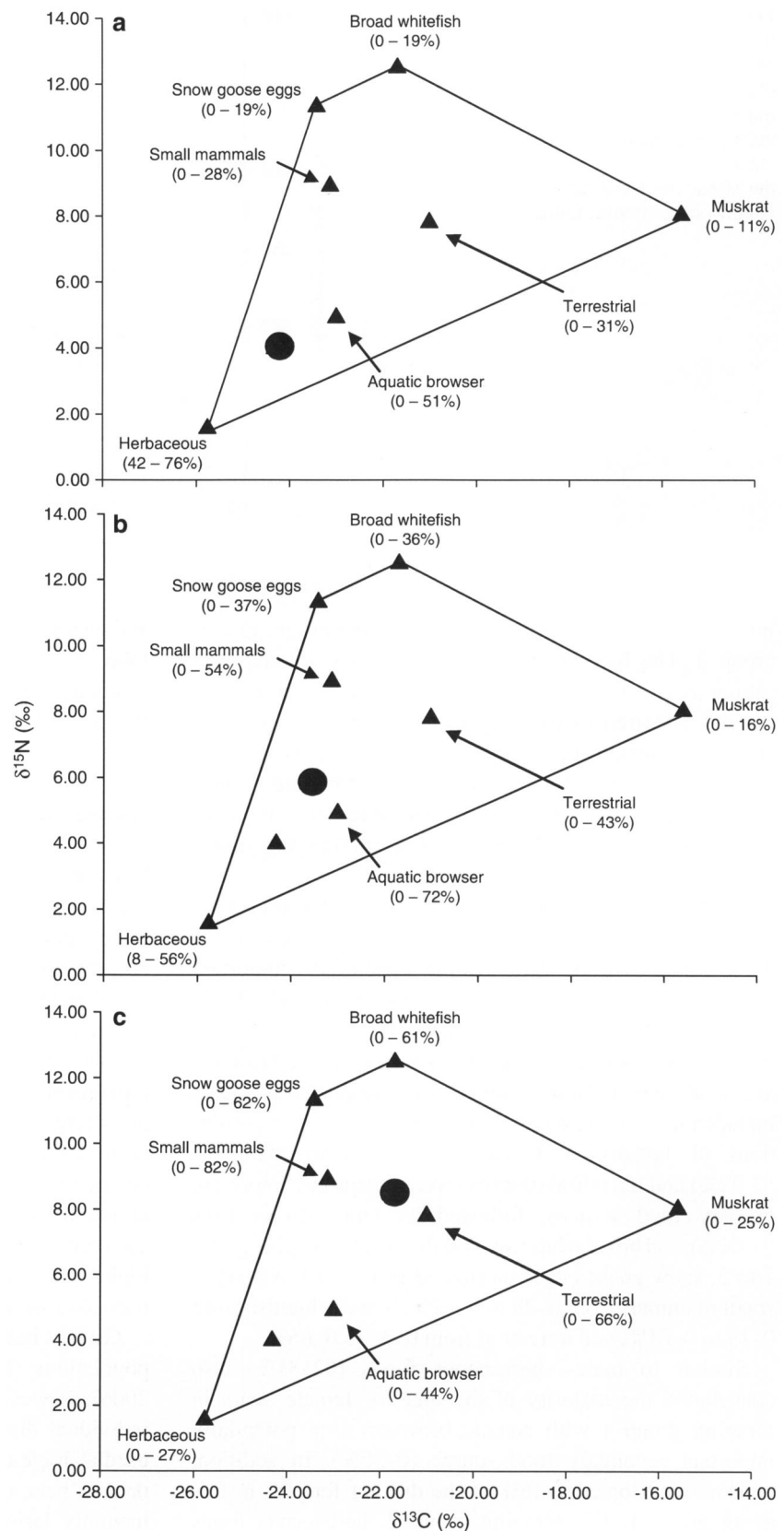
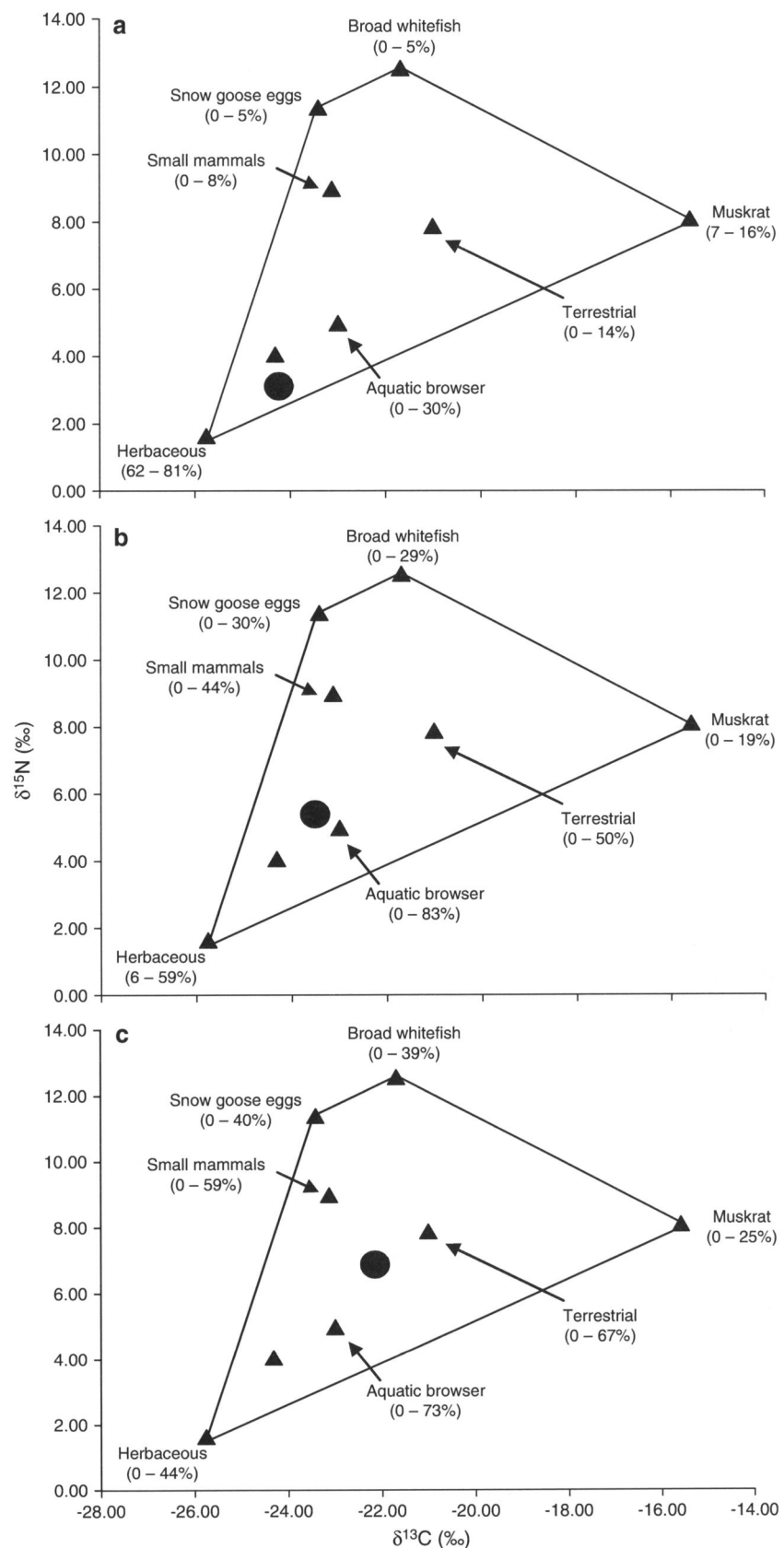


Fig. 6 Mixing polygon for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) of seven food sources (black triangles) for female grizzly bears sampled from 2003 to 2006 ($n = 27$) in the Mackenzie Delta region, Northwest Territories, Canada. Percentile ranges (1–99th percentile) show feasible contributions from each source to the mixture (black circles) for **a** the more herbivorous, **b** the omnivorous, and **c** the more carnivorous female bear



similar at $+2.9 \pm 0.9\%$ (Alves-Stanley and Worthy 2009). Based on the results of feeding trials of American black bears (*U. americanus*) conducted by Hilderbrand et al. (1996), which showed low between-individual isotopic variance, we are confident that the intrapopulation variation in $\delta^{15}\text{N}$ that we recorded for wild bears was representative of actual isotopic differences in diet and trophic differences in foraging behavior, and was not due to inherent population variance.

Diet specialization within populations may be driven by age- or sex-related factors or differences among ecologically heterogeneous individuals (Schoener 1986; Lima and Magnusson 1998; Shine et al. 2002; Bolnick et al. 2003). Because hair and claw samples included in our analysis were only from adult bears, we conclude that the observed diet specialization was not related to ontogenetic shifts, as bears matured from juveniles to adults (Polischuk et al. 2001; Newsome et al. 2006). Equally, because three foraging groups were identified for both males and females, we can also conclude that the occurrence of diet specialization was not limited by sexual dimorphism or body size and the ability to secure and handle prey (Selander 1966; Brown and Lasiewski 1972). What did differ for male and female bears was the proportional contributions of the seven source food types to their diets, with males potentially exploiting more animal protein, be it terrestrial, avian or aquatic. For sexually dimorphic species like grizzly bears, the nutritional needs of larger males are greater than those for females, which can result in increased carnivory for males compared to females (Jacoby et al. 1999). Conversely, because of their smaller size and reduced nutritional needs, females can select poorer quality yet adequate food resources (Rode et al. 2006). Therefore, we suggest that the individual diet specialization and trophic level variation that we observed for male and female bears resulted from interindividual differences in prey availability and foraging ability among bears. Similar patterns have been observed in several species. Svanback and Bolnick (2007) demonstrated that the level of diet specialization within a population of three-spine sticklebacks (*Gasterosteus aculeatus*) may vary depending on changing ecological attributes, with diet specialization increasing with the time it took to detect a change in prey availability. Urton and Hobson (2005) reported that the variable foraging behavior observed among wolves (*Canis lupus*) resulted from differences in the availability of foods specific to home ranges, which resulted in isotopic variation and dietary specialization among individuals. Also, a single population of ring-tailed lemurs (*Lemur catta*) was divided into three foraging groups based on diet specialization in their use of available forage in habitats that ranged from forested to open (Loudon et al. 2007).

It follows that along with variation in prey availability, diet specialization may result from phenotypical trade-offs due to individual-level morphological, physiological, and/or behavioral attributes and experiences that allow different individuals to be more effective at exploiting one type of prey and less effective at exploiting another (Robinson et al. 1996; Svanback and Bolnick 2005, 2007). The use of all resources by all members within a population's niche width is thus reflected in these trade-offs to the extent that subsets of diet specialization develop within the population (Bolnick et al. 2003). If bears are foraging optimally, they should maximize energy intake and may even ignore preferred prey items when searching and handling time make it more economical to seek alternate prey items (MacArthur and Pianka 1966; Stephens and Krebs 1986). Optimal foraging theory, therefore, provides added explanation for individual-level diet specialization if individuals differ phenotypically in their ability to exploit alternate prey types, and these individuals are able to add different prey types more effectively (Bolnick et al. 2003; Svanback and Bolnick 2005). Therefore, where prey density is low, two or more phenotypically different groups of consumers that rely on divergent alternate prey types will increase the population's niche width (Svanback and Bolnick 2007).

The Mackenzie Delta is characterized by low productivity and low availability of high-quality protein sources (Hilderbrand et al. 1999), and bear densities in this region are some of the lowest in North America (Nagy and Haroldson 1990). For an omnivore like the grizzly bear with a broad niche width and a high level of phenotypic variation, it is not surprising that individual-level diet specialization is more pronounced than for species with narrower niche widths (Lister 1976; Roughgarden 1979; Araujo et al. 2007). High levels of diet specialization and patterns of greater intrapopulation variation in foraging have been reported for other taxa with such characteristically wide niche widths (Lister 1976; Roughgarden 1979; Werner and Sherry 1987; Estes et al. 2003; Svanback and Bolnick 2007). In a review by Bolnick et al. (2003), the high occurrence of intrapopulation variation in foraging behavior across taxa suggests that the presence of diet specialization within populations may be a more general pattern than previously considered.

Although we failed to find a significant relationship between home range size and trophic position for the bears of the Mackenzie Delta, our results did provide support for the suggestion of Gittleman and Harvey (1982) and Mace et al. (1983) that omnivores with a higher proportion of animal protein in their diet should have higher rates of movement as they search for low-density animal prey. More herbivorous animals should have lower movement rates, which suggest that they are able to meet their nutritional needs by foraging slowly through a landscape of herbaceous

food sources. However, we found that a significant increase in movement rate with trophic position was only present among female bears, and only when examined using linear regression. The nonsignificant relationship that we observed between the movement rate and females by foraging group probably resulted from the low number of bears in each group, especially foraging group 3. Equally, the nonsignificant results that we observed when movement rate was analyzed by male trophic position were due to the small sample size. Given these variable results, we feel that further examination of the relationship between trophic position and range use is warranted.

The correlation between movement and trophic position that we observed is consistent with findings by Edwards et al. (2009) on the movement patterns and level of site fidelity relative to forage availability for grizzly bears in our study area. In landscapes with low productivity and available protein, and low spatial–temporal predictability of forage resources (i.e., low prey density), a flexible pattern of resource use and a low level of site fidelity is more adaptive than high site fidelity (Switzer 1993; Edwards et al. 2009). As a result, grizzly bear home range location drifted between years and bears found themselves in constantly changing ecological conditions (Edwards et al. 2009). In contrast, bears that live along the Pacific coast of North America have high levels of circannual site fidelity for protein-rich salmon (*Oncorhynchus* spp.) spawning streams, which are perennially reliable and consistent sources of high-quality forage (Gende and Quinn 2004; Mowat and Heard 2006). Therefore, in the Mackenzie Delta, grizzly bears benefit from a flexible foraging behavior that allows them to switch to different alternate prey that provide greater energy return for search and handling efforts. Which of the alternate prey types is selected may be defined by the phenotypical attributes and experiences of the individual, and this results in diet specialization and increased niche width (Robinson et al. 1996; Svanback and Bolnick 2005, 2007).

Understanding a species' niche width (Hutchinson 1957) and flexibility in foraging behavior is fundamental to effective conservation and management (Fuller and Sievert 2001). For policy development, species conservation is often based on the delineation of population-based resource needs, which is simplified to a broad definition of what is "typical" (Bolnick et al. 2003). By simplifying to such broad definitions, however, we may fail to identify the needs of certain segments within a population. Broadly classifying the diet of omnivorous species with relatively complex and not easily defined foraging behaviors may be particularly misleading. We suggest that by identifying different foraging behaviors within a population, we can improve the effectiveness of management programs by

improving our ability to refine protocols to meet the needs of focal groups and the population as a whole.

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