NICHE SEPARATION AMONGST SYMPATRIC URSIDS

RELATIVE TO SALMON USE

By

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      The members of the Committee appointed to examine the thesis of
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NICHE SEPARATION AMONGST SYMPATRIC URSIDS

RELATIVE TO SALMON USE

Abstract

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Historically, there were sympatric brown and black bears in much of North America prior to

European development. However, the two species did not evolve long-term together and dietary

overlap may be extensive. The re-establishment of brown bears in Idaho concurrent with salmon

recovery would benefit brown bears but may harm salmon if the total consumption by the two

ursids is additive. We hypothesized that there would be minimal dietary overlap between

sympatric brown bears (*Ursus arctos*) and American black bears (*U. americanus*) relative to

salmon utilization when alternative foods (e.g., berries or fruits) are available. To maximize

sensitivity of the test, we examined the diets of brown bears and black bears known to have

visited salmon streams on the Kenai Peninsula, Alaska. Species, sex, and individual

identification were determined by DNA analysis of hair and feces collected along salmon

streams. Assimilated diets were estimated from stable isotope analyses of hair. Assimilated

diets of brown bears were $66.0 \pm 16.7\%$ salmon, $13.9 \pm 7.5\%$ terrestrial animal matter, and 20.1

$\pm 17.2\%$ plant matter. Assimilated diets of black bears were $8.0 \pm 5.4\%$ salmon, $8.4 \pm 9.7\%$

terrestrial animal matter, and $83.6 \pm 7.7\%$ plant matter. Male and female brown bears did not

differ in either the proportion of dietary salmon ($62.1 \pm 16.9\%$ and $68.4 \pm 16.5\%$; $F = 0.35$, $P =$

0.5607), terrestrial animal matter ($16.7 \pm 9.9\%$ and $11.8 \pm 4.4\%$, $F = 1.38$, $P = 0.2504$), or plant

matter (21.1 ± 17.4 % and 19.8 ± 17.4 %, $F = 0.01$, $P = 0.9367$). Both sexes of brown bears

visited salmon streams and consumed significant amounts of salmon, but only male black bears

visited streams and then consumed minimal amounts of salmon. Thus, brown bears were largely

carnivorous ($79.9 \pm 17.2\%$ dietary animal matter). Black bears were largely

herbivorous/frugivorous ($83.6 \pm 7.7\%$ dietary plant matter) and, in the case of female black

bears, did not approach salmon streams. This lack of dietary overlap relative to salmon is

understandable in light of the dominance of brown bears over black bears, differing energy

requirements, and therefore their differing ability to efficiently exploit different food resources.

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CHAPTER ONE

INTRODUCTION

Much of western North America prior to European settlement had sympatric populations of brown bears and American black bears (Mattson et al. 2005). Because brown bears did not spread across western North America until approximately 13,000 years ago and thus have not evolved long-term with American black bears, dietary overlap amongst the two ursids can be extensive (Herrero 1978, Aune 1994, Jacoby et al. 1999, Hobson et al. 2000, Mattson et al. 2005). This potential competition may create difficulties when trying to re-establish or bolster remnant brown bear populations (Mattson et al. 2005).

The re-establishment of brown bears in central Idaho offers a unique challenge in that such bears historically fed on spawning salmon (Hilderbrand et al. 1996, USFWS 2000). However, brown bears are extinct and wild salmon are critically threatened in this ecosystem. Because brown bears feeding on salmon have larger litters and their populations are up to 50 times denser than those without salmon (Hilderbrand et al. 1999), the recovery of salmon in central Idaho would greatly benefit the recovery of brown bears. However, reintroduced brown bears would potentially compete with abundant black bears for salmon and other foods and thereby might reduce the chance for salmon recovery if total consumption by the two ursids is additive. In ecosystems without brown bears, black bears consume significant amounts of salmon (Reimchen 1998, Jacoby et al. 1999, Chi 1999). However, when both species are sympatric, brown bears can reduce salmon consumption by black bears and, thereby, might benefit salmon recovery when black bears are more numerous (Jacoby et al. 1999).

In quantifying the diets of sympatric brown bears and black bears on the Kenai Peninsula of Alaska, Jacoby et al. (1999) acquired hair samples for isotopic analyses from brown bears

known to have had access to salmon and from randomly selected, hunter-killed black bears. Because the black bear sample may have been biased by the unintentional inclusion of bears that did not have access to salmon, we initiated this study to examine the diets of both brown bears and black bears known to have visited salmon streams at a time when salmon were abundant.

We hypothesized that niche overlap between the two species would be highest when food resources are restricted in either quantity or quality, when food resources are dispersed and therefore not defendable, or when alternative food resources are not available. Because Kenai brown bears and black bears frequently have access to abundant, energy- and nutrient-dense salmon that are localized and defendable and berries that are widely dispersed, largely non-defendable, and more inline with the energetic demands of the smaller black bear (Welch et al. 1997), we hypothesized that niche overlap between the two ursids should be minimal relative to salmon utilization. Thus, the current study design, which compared diets of those bears that actually visited salmon streams, maximized the potential for dietary overlap and therefore sensitivity for testing the extent of niche overlap.

CHAPTER TWO

METHODS

Study Area

The Glacier and Seepage Creek study area is located in the Kenai National Wildlife Refuge on the southeast corner of Tustumena Lake, the largest lake on the Kenai Peninsula (Fig. 1). Access is by a 50 km boat ride. The streams are typical of small, forested salmon streams in south and southeast Alaska. Streams are short (Glacier Creek, 3.5 km and Seepage Creek, 0.6 km), narrow (mean = 7.7 m) and shallow (mean = 0.12 m). Sockeye salmon (*Oncorhynchus nerka*) return to Tustumena Lake via the Kasilof River from June through September to spawn in four main streams, Glacier Creek, Moose Creek, Bear Creek, and Indian Creek. Moose are the main potential mammalian prey for both brown bears and black bears (Schwartz and Franzmann 1991).

Vegetation at lower elevations is open and closed conifer forests of white spruce (*Picea glauca*) and black spruce (*P. mariana*) and deciduous forests of aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and cottonwood (*P. trichocarpa*). At mid-elevation the vegetation transitions to alders (*Alnus spp.*) and willows (*Salix spp.*), whereas high elevation sites are dominated by dwarf birch (*Betula nana*), willows, Labrador tea (*Ledum spp.*), and various berry or fruit producing shrubs (alpine blueberry (*Vaccinium uliginosum*), crowberry (*Empetrum nigrum*), low-bush cranberry (*Vaccinium vitis-idaea*), high-bush cranberry (*Viburnum edule*), American devilsclub (*Oplopanax horridus*), rose (*Rosa acicularis*), and Sitka mountain ash (*Sorbus sitchensis*)). Herbaceous vegetation includes sedges (*Carex spp.*), cotton grass (*Eriophorum spp.*), and bluejoint reedgrass (*Calamagrostis canadensis*).

The Kenai Peninsula brown bear population is estimated at 250 to 300 (DelFrate 1999) and black bears at 3000 to 4000 (McDonough 2005). Thus, black bears outnumber brown bears by at least 10 to 1. Both species are hunted with brown bear mortality from all causes limited to 15 bears. The black bear season is open year-round with a bag limit of two per year (Farley et al. 2001).

Capturing Brown Bears and GPS Mapping

Five adult female brown bears were captured in 2002, 2003 and 2004 and fitted with Global Positioning System (GPS) radio collars (Telonics, Mesa, AZ). Four of the bears were the same during all three years, and one was different each year. Bears were immobilized from a helicopter using Telazol (5-10 mg/kg; Taylor et al. 1989). Collars recorded the bears' locations every 13 minutes. Spring captures occurred during the middle of May and fall captures during the middle of October. All bears were weighed using a tripod and electronic load cell (± 0.2 kg). Hair samples were collected from each bear to determine annual diet by stable isotope analyses. Body composition was determined using isotopic water dilution (Farley and Robbins 1994; Hilderbrand et al. 1998).

Glacier and Seepage Creek locations were mapped by walking both creek edges with a GPS survey unit (accuracy of ± 1 m). Surveyed data were imported into ArcInfo (ESRI, Redlands, CA) and converted into polygons. A 10 m buffer was placed around each stream to account for collar error. Major berry fields were identified from earlier habitat maps (Ducks Unlimited 1999) and confirmed by ground surveys. GPS locations of each collared bear were queried to identify all daily locations within salmon or berry resource areas.

Measuring Food Availability

Salmon and berry availability were quantified from July 1 to October 1, 2003 and 2004. The number of salmon entering Glacier Creek during daylight hours was determined by mounting a solar-powered video camera 2.7 m above the creek's mouth. Images were recorded on videotape at 2 frames/sec. Because counts were limited by daylight which ranged from 14 to 20 hrs, the total daily fish estimates were corrected to 24-hr counts by assuming that the number of fish entering the stream per hour was the same during day and night. Similar counts could not be conducted on Seepage Creek because of high stream turbidity. Daily availability of live salmon in Glacier Creek was calculated by correcting 24 hour video counts for an average stream residence time of 10.8 days and a loss of 65% of live salmon to bears (Woody 1998). Although these estimates were from an earlier study, use of similar techniques during the current study produced a bear consumption estimate of 68% (Rode and Fortin, unpublished). The entirety of both Glacier Creek and Seepage Creek were walked once per week and all live and dead salmon counted. Three live female and male salmon were collected weekly for nutritional analyses.

Berries were sampled biweekly at sites known to be used by bears. Within each sampling area, 20 random 4 m^2 plots were examined for the presence or absence of ripe berries of alpine blueberry, low-bush cranberry, crowberry, and mountain ash. Within each plot, five subplots, 0.5 m^2, were randomly selected and the number of berries of each species counted, harvested, and wet weight determined. All berries of the same type were pooled for each collection date and analyzed for nutritional content.

Identification of bears using the stream corridor

Hair and feces were used to identify the number of individual brown bears and black bears visiting Glacier and Seepage Creeks during 2003 and 2004. All bear feces encountered within 10 m of the stream banks were collected weekly. Feces voided since the last walk (i.e.,

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within 7 days) were collected and homogenized, and 3 mls of the homogenate was stored in 90% ethanol with a 1(feces):4(ethanol) ratio at room temperature (Wasser et al. 1997). All samples were subsequently extracted within six months after field collection using a protocol for isolation of DNA from human feces (QIAamp DNA stool mini kit, Qiagen Inc., Valencia, CA).

Hair samples were collected from rub trees and from barbed-wire placed across trails. Hair was placed in a small sealed envelope and stored in a bag containing silica gel (Roon et al. 2003). A QIAamp DNA mini kit was used to extract DNA within 6 months of collection from hair samples that contained up to 15 follicles when possible. To reduce the risk of contamination, all scat and hair extractions were done in a separate laboratory dedicated to low-concentration degraded DNA that was physically isolated from other laboratories and which did not contain concentrated DNA (polymerase chain reaction product for blood and tissue extracts). One or more negative controls were included in each extraction to monitor for contamination.

Species identification was done using a 146 bp mtDNA segment as described in Murphy et al. (2000). PCR products were separated by size on an ABI 377 (Applied Biosystems, Foster City, CA) and scored using Genescan 3.0 and Genotyper 3.5. Seven variable loci of nDNA were used to determine individual identification for brown bears with a probability of identity value of < 0.005. The seven loci were divided into two multiplexes. The conditions for PCR I were a 15 µl reaction consisting of: 2.5 mM $MgCl_2$, 1X Gold Buffer, 0.1 µM each primer (G1A, G10B, and G10C), 1.3 µM each primer (G10D), 0.117 µM each primer (G10L), 0.5 units Amplitaq Gold DNA polymerase (Perkin-Elmer), 0.08 mM each dNTP, and 2 µl template. The conditions for PCR II were a 15 µl reaction consisting of: 2.5 mM $MgCl_2$, 1X Gold Buffer, 0.5 µM each primer (G10H and UarMu50), 0.5 units Amplitaq Gold DNA polymerase (Perkin-Elmer), 0.08 mM each dNTP, and 2 µl template. A thermal cycler (MJ Research, Waltham, MA) was used as follows:

initial 10m at 95°C, then cycles 55 of 30s at 95°C, 30s at 57.5°C (G1A, G10B, G10C, G10D,

and G10L) or 51°C (UarMu50 and G10H), and 40s at 72°C. PCR products were separated by

size on an ABI 377 and scored using Genescan 3.0 and Genotyper 3.5.   Individual black bears

were identified with similar methods and seven loci (G1A, G10B, G10C, G10D, G10L, G10M,

and G10P). The success rate for species identification was 94% for feces (176 samples), 71% for

all hair samples (175 samples), and 85% for hair samples with follicles (145 samples).

Sex identification was done on all hair samples using the primers and methods of Ennis

and Gallagher (1994). The final PCR volume for sex ID was 20 µl consisting of: 1.4 mM

MgCl$_2$, 1X Gold Buffer, 0.48 µM each primer (SE47 and SE48), 1.6 units Amplitaq Gold DNA

polymerase (Perkin-Elmer), 0.05 mM each dNTP, and 5.6 µl template. A thermal cycler was

used as follows: initial 10m at 95°C, then cycles 45 of 30s at 95°C, 30s at 44°C, and 40s at 72°C.

PCR products were separated by size on an ABI 377 and scored using Genescan 3.0 and

Genotyper 3.5. To ensure accuracy, all samples were genotyped a minimum of two times. The

success rate for sex identification of samples identified to species was 89%.

Dietary and nutritional analyses

Assimilated diets were estimated by stable isotope analyses (δ^{13}C and δ^{15}N) of all hair

samples collected during capture or remotely via hair snares that were identified to species and

sex by DNA analyses. Hair samples identified from the same individual bear were pooled for

isotope analyses. Major dietary items (moose, sockeye salmon, and berries and herbage) were

analyzed to determine their isotope concentrations. Hair samples were washed to remove oils

with a 2:1 chloroform:methanol mixture, dried, and weighed into 30 mm x 30 mm tin squares

(Elemental Microanalysis, Mt. Laurel, NJ). All food samples were freeze-dried, ground and

loaded into 5 mm x 9 mm tin capsules (Costech Analytical, Valencia, CA). A Carlo Erba

elemental analyzer interfaced with a Thermo-Finnigan Delta Plus XL mass spectrometer or a Micromass Optima mass spectrometer was used to analyze all samples via continuous flow-isotope ratio mass spectrometry (Fry et al. 1992). Isotopic compositions of $\delta^{13}C$ and $\delta^{15}N$ are reported as parts per thousand (‰) relative to VPDB and AIR, respectively, using the internationally distributed standards USGS 40 ($\delta^{13}C$ = -26.2‰, $\delta^{15}N$ = -4.5‰) and USGS 41 ($\delta^{13}C$ = 37.8‰, $\delta^{15}N$ = 47.6‰). Analytical error was ± 0.2‰ for C and N.

The IsoSource program (Phillips and Gregg 2003) was used to calculate the source contributions of food sources to brown and black bears by species and sex (http://www.epa.gov/wed/pages/models.htm). IsoSource allows for each possible solution of sources, summing to 100%, when there are more than $n + 1$ food sources and n isotopic ratios. The food resources used in the model were: sockeye salmon, moose, and plant matter. Food resources that did not differ significantly in isotopic values and were logically related (e.g., spawned and unspawned salmon and berries and other plant matter) were pooled a priori (Phillips et al. 2005). Food source isotopic values were corrected for tissue-diet discrimination prior to use in IsoSource. Nitrogen discrimination was corrected using the regression of Felicetti et al. (2003) while an average carbon discrimination of 3.7 ± 1.3 was used for all foods (Hilderbrand et al. 1996, Ben-David and Schell 2001, Felicetti et al. 2003).

All food samples were freeze-dried and ground. Samples were analyzed for protein content using a carbon-nitrogen TruSpec Analyzer (LECO Corporation, St. Joseph, MI) and gross energy by bomb calorimetry. Total dietary fiber (TDF) was determined using the Prosky et al. (1984) method (Sigma Product #: TDF-100A0) as modified by Pritchard and Robbins (1990). TDF and gross energies of berries were used to estimate their digestible energy content (Pritchard and Robbins 1990). All values are reported on a 100% dry matter basis.

Statistical Analyses

Mean isotope signatures for similar food items were compared using a student's t-test. ANOVA was used to test for differences between the carbon and nitrogen isotopic signatures of the dietary components and hair by species, sex, time of collection, and year (PROC GLM; SAS 2003). To compare differences in brown bear foraging patterns from mid-July to mid-September to that of early October, a Cochran test for unequal variances was utilized. Paired-comparison of collared females between years was done using repeated measures ANOVA (SAS 2003).

CHAPTER THREE

RESULTS

The timing of salmon and berry availability overlapped and allowed brown bears and black bears to choose between these two major fall foods. Salmon first became available mid-July and peaked in late August (Fig. 2). Maximum, one-day live and dead salmon numbers were 28,000 in Glacier Creek and 535 in Seepage Creek. Ripe fruits and berries were available in abundance by mid-July and continued into October after salmon had disappeared. Fruit and berry density was quite variable between years and areas, but averaged 14 ± 47 per m^2. Salmon contained over 20 times more protein and over twice as much digestible energy as berries on a fresh weight basis (Table 1).

Thirty-three individual brown bears and 17 black bears utilized the stream corridors during 2003 and 2004. Brown bears represented 76% of all bears in 2003 and 63% in 2004. Males of both species were most common, with 63% of the brown bears and 100% of the black bears being male. The GPS-collared, adult female brown bears began visiting Glacier and Seepage Creeks up to two weeks before salmon arrived, at which time the vegetation growing in bear trails along the streams became compacted by increasing bear traffic. Total time that brown bears spent at the stream declined concurrent to the decline in salmon numbers (Figs. 2 and 3). However, as the season progressed, the number of black bears visiting the stream declined faster than brown bears such that the relative proportion of brown bears increased from August to October (Fig. 4). Time spent in delineated berry fields by the collared brown bears averaged 14 $\pm$ 13% of the day from mid-July to mid-September when salmon were abundant, but increased to $31 \pm 27\%$ by early October ($t = -3.55$, $P = 0.0014$). The collared, adult female brown bears weighed 141 ± 21 kg ($12.0 \pm 2.8\%$ fat) in the spring and 239 ± 20 kg ($31.1 \pm 1.7\%$ fat) in the fall.

Brown bears had a significant marine dietary component based on hair isotopic signatures (Fig. 5). There were no significant differences between the isotopic signatures of brown bear hair snared from July through September and fully-grown hair collected in either May or October from the collared bears ((δ^{13}C, F = 0.94, P = 0.3406; δ^{15}N, F = 0.03, P = 0.8547) (Fig. 5). There were no significant differences between years in the isotopic signatures or assimilated diets of the four adult female brown bears captured during all three years (salmon, F = 0.11, P = 0.4930; terrestrial meat, F = 0.36, P = 0.7092; plant matter, F = 0.69, P = 0.5277). Because there were no significant differences between years in the isotope signatures of either brown bears or black bears (δ^{13}C, F = 1.55, P = 0.2322; δ^{15}N, F = 2.16, P = 0.1368), all data were combined within a species.

Mean, brown bear isotope signatures were -19.3 ± 0.8‰ (δ^{13}C) and 11.5 ± 1.8‰ (δ^{15}N) and for black bears -21.6 ± 1.4‰ (δ^{13}C) and 6.0 ± 2.9‰ (δ^{15}N). The corresponding assimilated diet estimates for brown bears were 66.0 ± 16.7% salmon and 20.1 ± 17.2% plant matter and for black bears 8.0 ± 5.4% salmon and 83.6 ± 7.7% plant matter (salmon, F = 56.29, P < 0.0001; plant matter, F = 58.94, P < 0.0001). The dietary proportion of terrestrial animal matter was 13.9 ± 7.5% for brown bears and 8.4 ± 9.7% for black bears (F = 2.74, P = 0.1143). Male and female brown bears did not differ in either the proportion of dietary salmon (62.1 ± 16.9% and 68.4 ± 16.5%; F = 0.35, P = 0.5607), terrestrial meat (16.7 ± 9.9% and 11.8 ± 4.4%; F = 1.38, P = 0.2504), or plant matter (21.1 ± 17.4% and 19.8 ± 17.4%, F = 0.01, P = 0.9367).

CHAPTER FOUR

DISCUSSION

The assimilated diet estimates for salmon use by sympatric brown bears (66.0 ± 16.7%) and black bears (8.0 ± 5.4%) are similar to those of Jacoby et al. (1999) (50 ± 33% and 0 ± 0%, respectively). Thus, even though black bears were seen in and immediately adjacent to streams brimming with salmon, their use of salmon when sympatric with brown bears was negligible. During an observational study of sympatric brown bears and black bears at Wolverine Cove and Creek on the Alaska Peninsula, black bears moved through the area very quickly and captured less than 1% of all fish taken by bears (Tollefson et al. 2005). The complete absence of female black bears in our DNA identifications of feces and hair collected along Glacier Creek and Seepage Creek is identical to an earlier study in which foot snares were used to capture bears along these creeks. Ten male black bears, 6 to 10 yrs old and weighing ~100 kg, and no females were captured (Farley, Alaska Department of Fish and Game, unpublished). Thus, even though the Kenai Peninsula has brown bear densities one-tenth those of black bears, the presence of brown bears on salmon streams is sufficient to virtually eliminate use of salmon by black bears in those areas.

The minimal use of salmon by black bears leads to black bears being largely herbivorous/frugivorous (83.6 ± 7.7% plant matter) as compared to the largely carnivorous brown bears (79.9 ± 17.2% animal matter). Because the diets of black bears determined in this study were for only those male bears that actually visited a salmon stream, the reliance of black bears within the larger population on plant matter is probably underestimated. For example, the assimilated diet of black bears that did not visit salmon streams would be 90.9% plant matter and

9.1% terrestrial animal matter if they had the same dietary ratio of plant matter to terrestrial animal matter as black bears that consumed salmon.

The niche separation between brown bears and black bears in using salmon and plant matter is presumably due to 1) the dominance of brown bears over black bears (Craighead et al. 1995), 2) the increased energetic requirement of larger, adult brown bears that makes salmon utilization obligatory (Robbins et al. 2004), and 3) the reduced energetic demand of the smaller black bears and the availability of alternative foods (i.e., fruits and berries) of a quantity and quality sufficient to meet their needs (Welch et al. 1997). The exception to the above constraints would be brown bear females with dependent young that may also temporally avoid salmon streams because of the risk of infanticide (Ben-David et al. 2004).

This niche separation between current day brown bears and black bears relative to salmon utilization is likely similar to the hypothesized niche separation between the highly carnivorous, but extinct, short-faced bear (*Arctodus simus*) and the ancestors of today's black bears (Brown 1993, Matheus 1995). Thus, black bear avoidance of nutrient-dense salmon because of the presence of a more dominant, carnivorous ursid may have a much longer evolutionary history than the current brown bear-black bear interaction.

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Table 1. Nutritional analyses of salmon and major berries and fruits. The berry and fruit analyses include the seeds, which may or may not be digestible. See Welch et al. (1997) for analyses without seeds.

Food	Dry matter (%)	Crude protein (% dry matter)	Gross energy (kcal/g dry matter)	Digestible Dry Matter (%)
Sockeye salmon	24.1 ± 3.2	79.2 ± 4.4	5.17 ± 0.28	92.8 ± 0.8
Alpine blueberry	14.3 ± 1.1	4.8 ± 3.4	4.70 ± 0.24	74.5 ± 1.9
Crowberry	16.9 ± 2.8	5.4 ± 3.3	5.02 ± 0.21	48.1 ± 8.7
High-bush cranberry	17.7 ± 2.7	7.6 ± 5.7	5.03 ± 0.28	44.7 ± 9.8
Low-bush cranberry	21.9 ± 5.4	3.6 ± 1.4	4.69 ± 0.10	68.4 ± 2.9
Sitka mountain ash	30.5 ± 8.1	8.3 ± 1.0	4.92 ± 0.16	40.4 ± 4.7
Rose hips	32.7 ± 4.7	8.6 ± 1.6	4.84 ± 0.16	29.5 ± 6.2
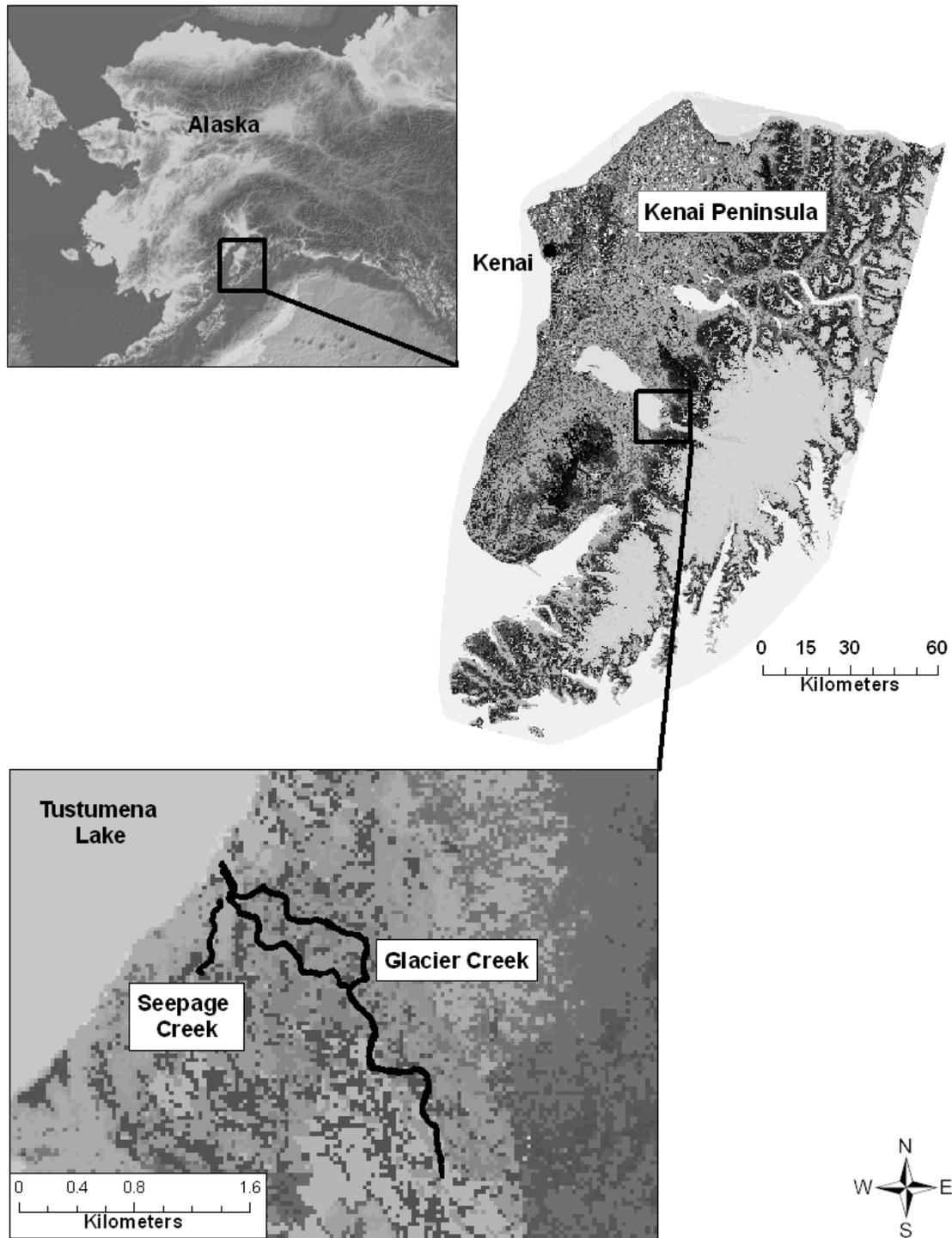
Figure 1. The location of the study area at Glacier Creek and Seepage Creek, Alaska.
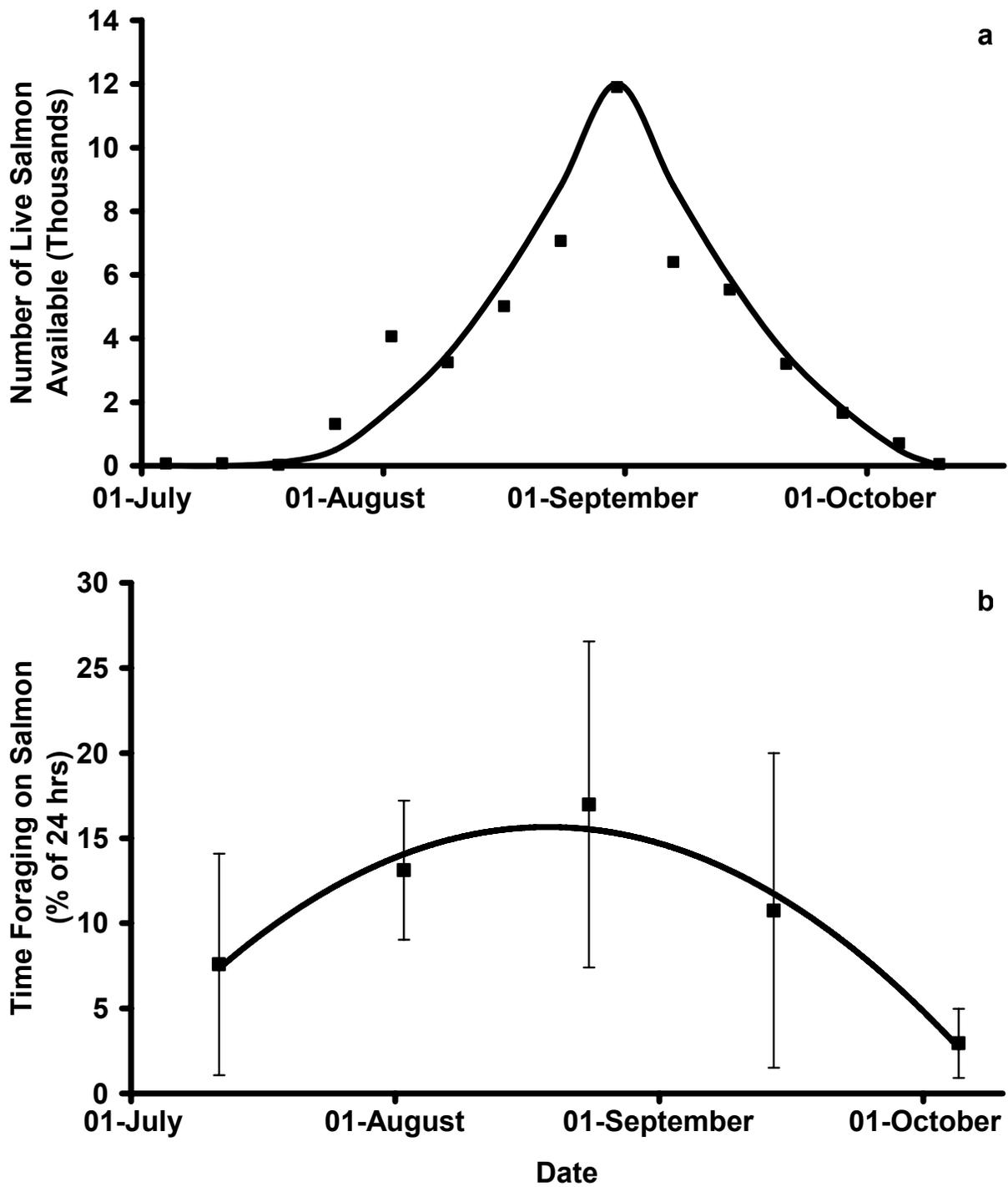
Figure 2. (a) The number of live salmon in Glacier Creek, Alaska during 2003 and 2004. Line

fitted by eye. (b) Time spent by GPS-collared, adult female brown bears in or

immediately adjacent to Glacier Creek or Seepage Creek, Alaska in 2002, 2003 and 2004.
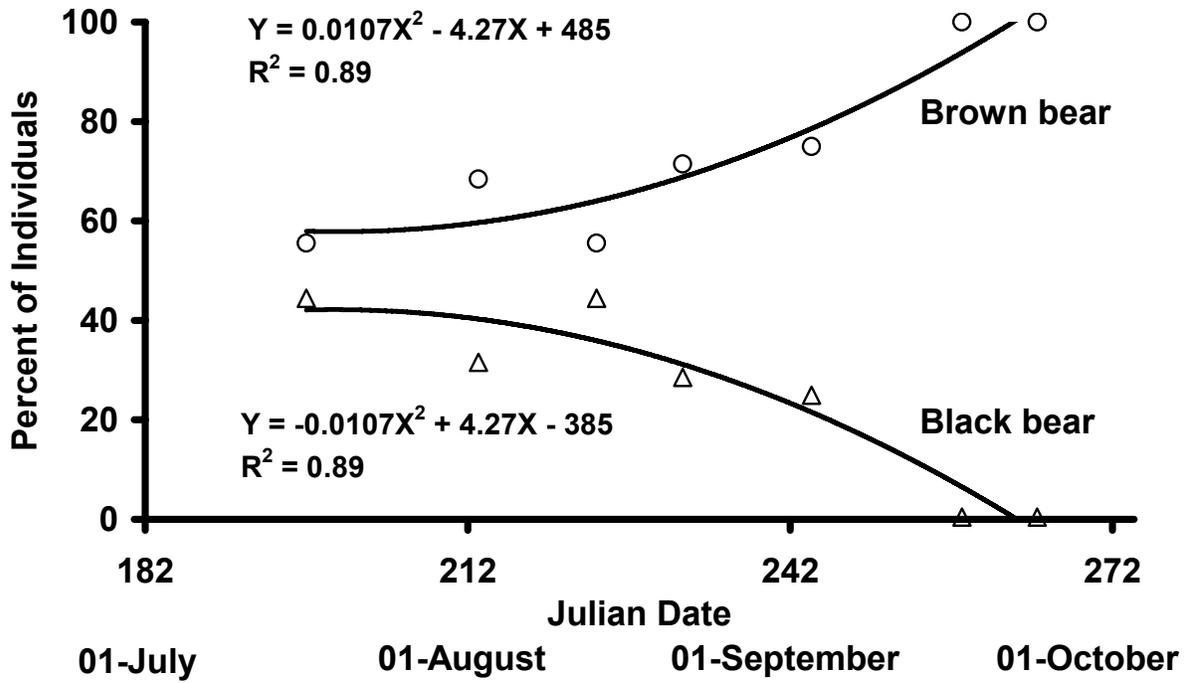
Figure 3. The relative proportion of brown bears and black bears visiting Glacier Creek and

Seepage Creek, Alaska during the spawning salmon run in 2003 and 2004.
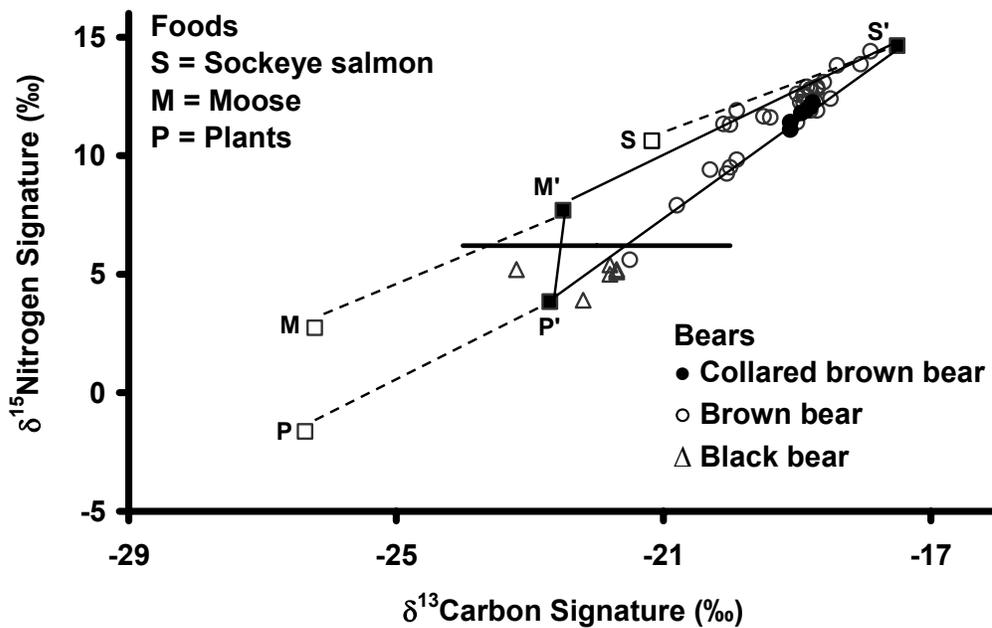
Figure 4. Isotopic signatures for bear hair samples collected during capture or on hair-snares

along Glacier Creek and Seepage Creek, Kenai Peninsula, Alaska during 2002, 2003 and

2004. Mean isotopic signatures are given for the main food sources and are denoted with

letters. Corrections for diet-tissue discrimination of food sources are indicated by prime

letters at the end of the dashed lines. The solid line represents a cutoff point at 6.2‰ for

$\delta^{15}N$, below which there is less than 10% contribution from salmon (Ben-David et al.

2004).