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Authors: Fortin, Jennifer K., Farley, Sean D., Rode, Karyn D., and Robbins, Charles T.

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# Dietary and spatial overlap between sympatric ursids relative to salmon use

Jennifer K. Fortin<sup>1,5</sup>, Sean D. Farley<sup>2</sup>, Karyn D. Rode<sup>3</sup>, and Charles T. Robbins<sup>4</sup>

<sup>1</sup>*School of Biological Sciences, Washington State University, Pullman, WA 99164-4236, USA*

<sup>2</sup>*Division of Wildlife Conservation, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, USA*

<sup>3</sup>*US Fish and Wildlife Service, Marine Mammals Management, 1011 East Tudor Road, Anchorage, AK 99503, USA*

<sup>4</sup>*Department of Natural Resource Sciences and School of Biological Sciences, Washington State University, Pullman, WA 99164-4236, USA*

**Abstract:** We hypothesized that there would be minimal dietary overlap between sympatric brown bears (*Ursus arctos*) and American black bears (*U. americanus*) relative to salmon (*Oncorhynchus* spp.) utilization when alternative foods (e.g., fruits) are abundant. To maximize the chance that we would reject this hypothesis, we examined the diets of brown and black bears known to have visited salmon streams. Species, sex, and individual identification of bears visiting salmon streams were determined by DNA analysis of hair and feces collected in 2002–2004 along those streams. Diets were estimated from fecal residues and stable isotope analyses of hair. Assimilated diets of brown bears were 66.0% (SD = 16.7%) salmon, 13.9% (SD = 7.5%) terrestrial animal matter, and 20.1% (SD = 17.2%) plant matter. Assimilated diets of black bears were 8.0% (SD = 5.4%) salmon, 8.4% (SD = 9.7%) terrestrial animal matter, and 83.6% (SD = 7.7%) plant matter. Male and female brown bears did not differ in either the proportion of dietary salmon, terrestrial animal matter, or plant matter. The relative amounts of fruit residues in the feces of brown bears (87.0%, SD = 15.2%) and black bears (91.8%, SD = 7.2%) did not differ. Both sexes of brown bears visited salmon streams and consumed significant amounts of salmon, but only male American black bears visited streams and then consumed minimal amounts of salmon. Thus, brown bears were largely carnivorous and black bears were largely herbivorous and frugivorous. This reduced dietary overlap relative to salmon and fruit use is understandable in light of the concentrated, defendable nature of salmon in small streams, the widely dispersed, non-defendable nature of abundant fruits, the dominance of brown over black bears, the higher energy requirement of the larger brown bear, and, therefore, the differing ability of the species to efficiently exploit different food resources.

**Key words:** American black bear, brown bear, diet, fruit, salmon, stable isotopes, *Ursus americanus*, *Ursus arctos*

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Much of western North America prior to European settlement had sympatric populations of brown bears and American black bears (Mattson et al. 2005). However, brown bears arrived relatively recently in North America (~13,000 years ago) and, thus, have not had a long coevolutionary history with black bears. Mattson et al. (2005) suggested that the extensive dietary overlap that can occur between brown bears and black bears is an expected outcome of their relatively short coevolu-

tion. However, the ancestors of today's black bears had a long evolutionary history with the highly carnivorous, large, and presumably dominant short-faced bear (*Arctodus simus*) that became extinct as brown bears entered North America (Brown 1993, Matheus 1995).

Therefore, we suggest that a more worthwhile approach to understanding dietary overlap and competitive advantages between brown and black bears will be based on understanding their differing absolute nutritional requirements due to the larger size of the brown bear, the spatial distribution of

<sup>5</sup>jfortin@wsu.edu

foods and whether they are concentrated and defendable or dispersed and largely non-defendable, anatomical specializations of each species that enable exploitation of different resources (such as digging capability of brown bears and climbing capability of black bears), and the social dominance of brown bears over black bears (Mattson et al. 1992, Welch et al. 1997, Hilderbrand et al. 1999, Rode et al. 2001, Gende and Quinn 2004, Mattson et al. 2005). For example, dietary and spatial overlap between brown and black bears should be highest when food resources are limited in either quantity or quality, when food resources are dispersed and therefore not defendable, and when alternative food resources are not available. Brown bears should dominate higher quality foods that are concentrated at predictable times and places (e.g., salmon runs; Mattson et al. 2005).

To further test these ideas, we explored dietary and spatial overlap between brown and black bears on the Kenai Peninsula relative to the consumption of salmon and fruit. Both brown and black bears when allopatric readily consume salmon (*Oncorhynchus* spp.; Frame 1974, Reimchen 1998, Jacoby et al. 1999, Gende et al. 2001, Gende and Quinn 2004, Mowat and Heard 2006). The Kenai Peninsula brown bear population is estimated at 250–300 (DeFrate 1999) and the black bear population at 3,000–4,000 (McDonough 2005). Thus, black bears likely outnumber brown bears by at least 10 to 1. Kenai brown and black bears frequently have access to abundant, energy- and nutrient-dense salmon that are localized and defendable and fruits and other plant matter that are widely dispersed, largely non-defendable, but commensurate with the energetic demands of the smaller black bear (Welch et al. 1997). Given the food availability and distribution, we hypothesized that dietary overlap between these ursids would be minimal relative to salmon utilization with brown bears being the primary consumer, but that both species would use fruits with black bears being the primary consumer.

The assimilated diets of sympatric brown and black bears have been previously quantified on the Kenai Peninsula (Jacoby et al. 1999). However, Jacoby et al. (1999) acquired hair samples for isotopic analyses from brown bears known to have visited salmon streams 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 brown and black bears known to have visited salmon streams when both salmon and fruits were abundant. This study design, in which diets of only those bears that visited salmon streams were compared, maximized the potential for dietary overlap in salmon consumption and therefore the sensitivity for testing our hypotheses.

## 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). Because access to the study area is by a 50-km boat ride, anglers and hunters are relatively uncommon. Both streams have abundant salmon, and brown and black bears are common in the immediate area. Both species are hunted, with annual brown bear mortality from all causes limited to 15 bears. The black bear season is open year-round with a bag limit of 2/year (Farley et al. 2001).

Glacier and Seepage Creeks are typical of many small, forested, salmon streams in south and southeast Alaska. These 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 4 main streams: Glacier Creek, Moose Creek, Bear Creek, and Indian Creek. Moose (*Alces alces*) are the main potential mammal prey for both 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 fruit-producing shrubs (alpine blueberry [*Vaccinium uliginosum*], crowberry [*Empetrum nigrum*], low-bush cranberry [*Vaccinium vitis-idaea*], high-bush cranberry [*Viburnum edule*], American devilscub [*Oplopanax horridus*], rose [*Rosa acicularis*], and Sitka mountain ash [*Sorbus sitchensis*]).

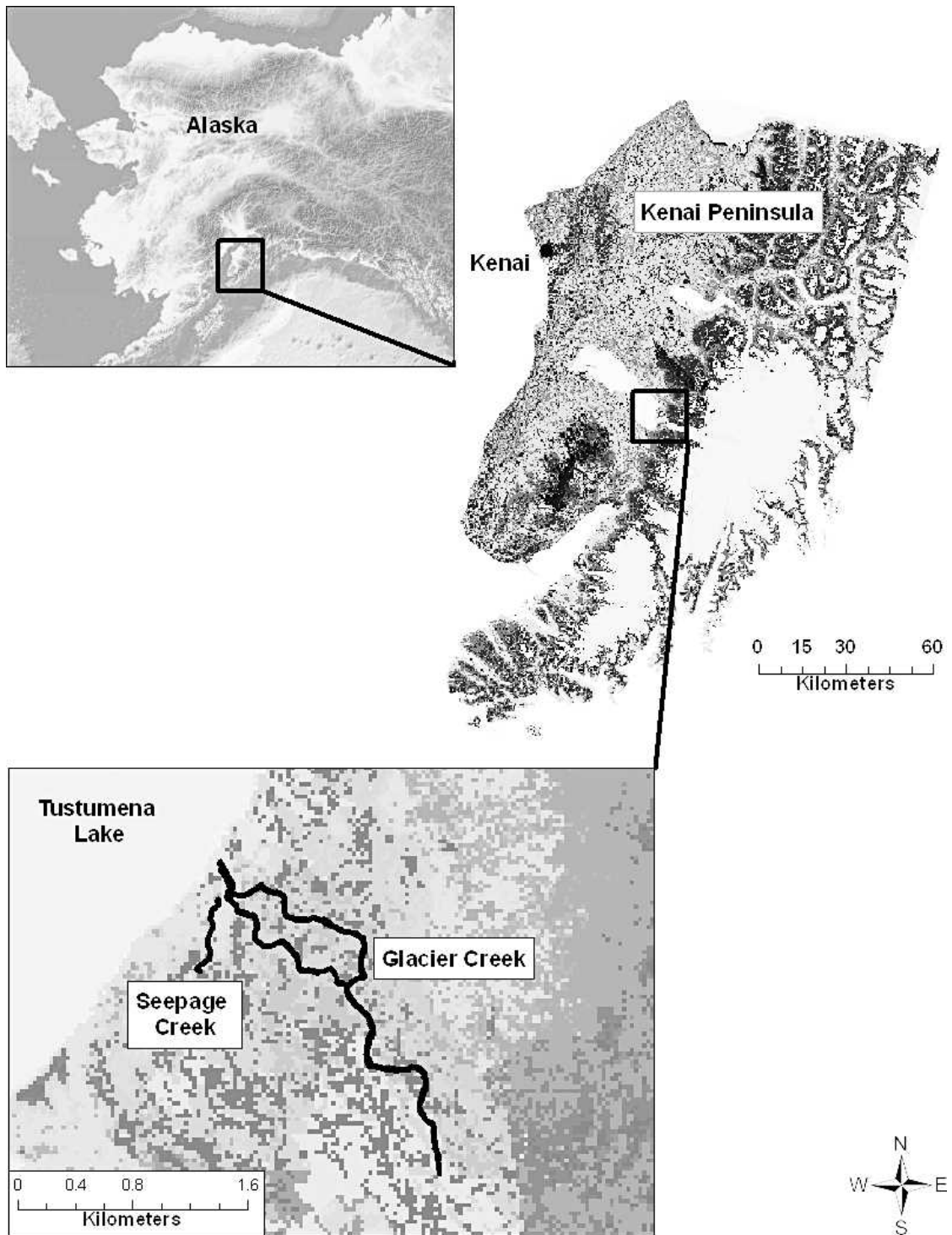


Fig. 1. Study area at Glacier Creek and Seepage Creek, Alaska, USA for a 2002–04 study of diet overlap between brown and black bears.



Herbaceous vegetation includes sedges (*Carex* spp.), cotton grass (*Eriophorum* spp.), and bluejoint reed-grass (*Calamagrostis canadensis*).

### **Capturing brown bears and sampling hair and feces**

We captured 5 adult female brown bears in 2002, 2003, and 2004 (Rode et al. 2007) and fitted them with global positioning system (GPS) radiocollars with an accuracy of 10 m (Telonics, Mesa, Arizona, USA). Females were prioritized for collaring because of their importance to population productivity and because females more readily retain collars than males due to their smaller neck to head ratio. Four of the bears were collared all 3 years while the fifth individual changed each year. We immobilized bears from a helicopter using tiletamine/zolazepam (5–10 mg/kg; Taylor et al. 1989). Collars recorded the bears' locations every 13 minutes. Spring captures occurred during the middle of May prior to molting the previous year's pelage, and fall recaptures occurred during the middle of October prior to denning and after the current year's hair growth was complete. All bears were weighed within 0.2 kg using a tripod and electronic load cell. Hair samples were collected from each bear to determine assimilated diet by stable isotope analyses. We determined body composition using isotopic water dilution (Farley and Robbins 1994, Hilderbrand et al. 1998).

Hair and feces collected along Glacier and Seepage Creeks in 2003 and 2004 were used to identify the minimum number of brown and black bears visiting the streams. Although we wanted to identify as many bears using the stream as possible, no attempt was made to estimate the total bear population. Both banks of each stream out to 10 m were searched weekly for bear feces. We collected samples of each defecation and stored them using methods of Wasser et al. (1997). Because the volume of fecal piles frequently exceeded what was necessary for DNA and fecal residue identification, the remaining feces were removed or marked to prevent future collection. We collected hair samples weekly from 7 sampling stations randomly distributed along each stream corridor. Each station consisted of either a rub tree wrapped with barbed wire, or barbed wire placed across well worn bear trails. The stations were unbaited. Each barb containing hair was treated as an independent capture event from which hair was placed in a small sealed envelope and stored in a bag containing silica gel (Roon et al.

2003). Any uncollected hair was burned to prevent future contamination.

### **GPS mapping**

We mapped Glacier and Seepage Creeks by documenting stream edges with a GPS unit (accuracy of 1 m). Surveyed data were imported into ArcInfo and converted into polygons. A 10-m buffer was extended beyond each stream bank to account for collar error and to map the stream corridor for fecal and hair collection. We identified major areas of fruit-producing plants from habitat maps (Ducks Unlimited, Inc. 1999) and confirmed them using ground surveys. GPS locations of each collared bear were queried to identify daily locations within salmon or fruit resource areas. We considered bears to be at the stream when a GPS collar location was within the stream corridor. Bears were considered to be foraging on fruit if the location was within delineated fruit resource areas and movement occurred as defined by differing sequential locations.

### **Measuring food availability**

We quantified salmon and fruit availability 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. Because of the shallowness of the stream, all fish were available to bears once they entered the stream. Images were recorded on videotape at 2 frames/sec. Because counts were limited by daylight (range = 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. We calculated daily availability of live salmon in Glacier Creek 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). We walked the entirety of both Glacier and Seepage Creeks weekly and counted all live and dead salmon observed. Three live salmon of both sexes were collected weekly for nutritional analyses.

We sampled fruits biweekly at sites known to be used by bears. Major fruit-producing sites were not

immediately adjacent to salmon streams and therefore required that bears leave the vicinity of the streams to forage on this resource. Within each sampling area, we examined 20 random 4-m<sup>2</sup> plots for the presence of ripe fruit of alpine blueberry, low-bush cranberry, crowberry, and mountain ash. Plots were randomly selected by GPS location within a 2.5-km<sup>2</sup> area identified as a fruit resource area. Within each plot, 5 subplots (0.5 m<sup>2</sup>) were randomly selected and the fruits of each species counted, harvested, and weighed. All fruits of the same type were pooled for each collection date and analyzed for dry matter and nutritional content.

### Genetic identification of bears

DNA was extracted from both feces (Qiagen stool kit) and hair (Qiagen mini kit) within 6 months of field collection (Qiagen Inc., Valencia, California, USA). When possible, we used at least 15 follicles for hair extraction (Roon et al. 2003) under non-invasive DNA (clean lab) laboratory protocols (Murphy et al. 2000). One or more negative controls were included in each extraction to monitor for contamination.

Species identification (ID) was accomplished using a mtDNA segment with a 13–20 base pair (bp) deletion in brown bears (146–151 bp) relative to black bears (163–164) (Shields and Kocher 1991, Waits 1996). Primers and polymerase chain reaction (PCR) conditions followed Murphy et al. (2000). Known brown bear and black bear samples and negative controls were included in each assay to ensure accuracy. 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).

Individual identification utilized microsatellite loci developed for brown and black bears (Ostrander et al. 1993; Paetkau et al. 1995, 1998; Taberlet et al. 1997). Seven nDNA microsatellite loci were used to identify individual bears (G1A, G1D, G10B, G10C, G10L, G10M, and G10P). The first 5 loci were annealed at 57.5°C and the latter 2 at 52.0°C for 45 cycles using Amplitaq Gold DNA polymerase (Qiagen Inc., Valencia, California, USA). Each assay contained a negative control and at least 1 known brown or black bear to ensure that no shift in alleles occurred. Samples for both species were considered successfully identified if values were acquired for all 7 loci. Loci were chosen based on probability of identity statistics ( $P_{ID}$ ), which is the probability that

in a given population 2 random individuals will have the same genotype (Waits et al. 2001). The  $P_{ID}$  was calculated for the Kenai Peninsula brown bear population from Jackson (2003) and for the black bear population from Robinson (2006) with a threshold value of 0.005 for identifying individuals. The success rate of individual identification for hair samples identified to species was 86%. Twelve individuals were positively identified more than once.

We conducted sex identification on all hair samples positively identified as either a brown or black bear using the primers and methods of Ennis and Gallagher (1994). For males, 2 fragments of 181–187 and 232–244 bp were observed while only 1 fragment of 232–244 bp was observed for females. Fecal samples were not used in sex identification because of the potential for false sex determination of females if male mammalian meat was consumed (Murphy et al. 2003). Each assay contained at least 1 negative control and 1 male and female bear as a positive control. To ensure accuracy, we genotyped all samples a minimum of 2 times for sex and individual identification. The success rate of sex identification for hair samples identified to species and individual was 89%.

### Dietary and nutritional analyses

We estimated assimilated diets by stable isotope analyses ( $\delta^{13}\text{C}$  [carbon] and  $\delta^{15}\text{N}$  [nitrogen]) for all hair samples collected during capture or remotely via hair snares that were identified to species, individual, and sex by DNA analyses. Hair samples identified from the same individual were pooled for isotope analyses. We analyzed major dietary items (moose, sockeye salmon, fruits, and herbage) to determine their isotope signatures. Hair samples and food items were prepared and analyzed as in Felicetti et al. (2003). Isotopic signatures are reported as parts per thousand (‰) relative to VPDB ( $\delta^{13}\text{C}$ ; Vienna peedee belemnite) and atmospheric N ( $\delta^{15}\text{N}$ ) using the internationally distributed standards USGS (US Geological Survey) 40 ( $\delta^{13}\text{C} = -26.2\text{‰}$ ,  $\delta^{15}\text{N} = -4.5\text{‰}$ ) and USGS 41 ( $\delta^{13}\text{C} = 37.8\text{‰}$ ,  $\delta^{15}\text{N} = 47.6\text{‰}$ ). Analytical error was 0.2‰ for both isotopes.

The IsoSource program (Phillips and Gregg 2003) was used to calculate the relative dietary 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 we 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 (spawned and unspawned salmon and fruits 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) and an average carbon discrimination of 3.7 (SE = 1.3) was used for all foods (Hilderbrand et al. 1996, Ben-David and Schell 2001, Felicetti et al. 2003).

We quantified the relative contribution of fruit and herbage to the feces produced by each species and collected along the stream corridor using microhistological analyses (Davitt and Nelson 1980, Holeček and Vavra 1981, Holeček and Gross 1982). Microhistological analyses were used rather than the more common fecal sorting and volumetric procedures (Schwartz and Franzmann 1991, Hewitt and Robbins 1996) to minimize subjectivity. All plant cuticle, epidermal fragments, fruit pulp and seeds, and animal residue were quantified in 25 randomly located views per slide and relative coverage of fruit and herbage material expressed as a percent of total fecal matter.

Salmon and fruit samples were freeze-dried and ground. We analyzed all samples for protein content using a carbon–nitrogen TruSpec Analyzer (LECO Corporation, St. Joseph, Michigan, USA) and gross energy by bomb calorimetry. Total dietary fiber (TDF) was determined using the Prosky et al. (1984) method (Sigma Product TDF-100A0, Sigma Chemical, St. Louis, Missouri, USA) as modified by Pritchard and Robbins (1990). TDF and gross energies of fruits 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 isotopic signatures for similar foods were compared using Student's *t*-test. ANOVA was used to test differences between the carbon and nitrogen isotopic signatures of the dietary components and the hair samples by species, sex, time of collection, and year (PROC GLM; SAS 2004). The time of collection test compared the isotopic signatures of the fully grown hair collected from captured brown

bears to the hair that was snared throughout the summer and fall to determine if dietary estimates differed (PROC GLM, Cochran test for unequal variances; SAS 2004). The numbers of individual brown and black bears visiting the stream corridor monthly were compared using ANOVA (PROC GLM; SAS 2004). Paired-comparisons of the annual assimilated diets of collared brown bears between years were tested using repeated measures ANOVA. A nonparametric 1-way ANOVA was used to test for differences in the relative proportions of fruit fecal residues between brown and black bears within years (SAS 2004).

### Results

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

Thirty-three individual brown bears and 17 black bears were identified within the stream corridors during 2003 and 2004. Brown bears represented 76% of all bears identified in 2003 and 63% in 2004. Males of both species were most common; 63% of brown bears and 100% of black bears were males. GPS-collared adult female brown bears began visiting Glacier and Seepage Creeks up to 2 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 collared brown bears spent at the stream declined concurrent to the decline in salmon numbers. However, as the season progressed, the number of individual black bears identified within the stream corridor declined faster than identified brown bears, such that the relative proportion of brown to black bears increased from August to October ( $n = 54$ ,  $t = 17.25$ ,  $P < 0.01$ ). Time spent in delineated fruit fields by collared brown bears averaged 14% (SD = 13%) of the day from mid-July to mid-September when salmon were abundant, but increased to 31

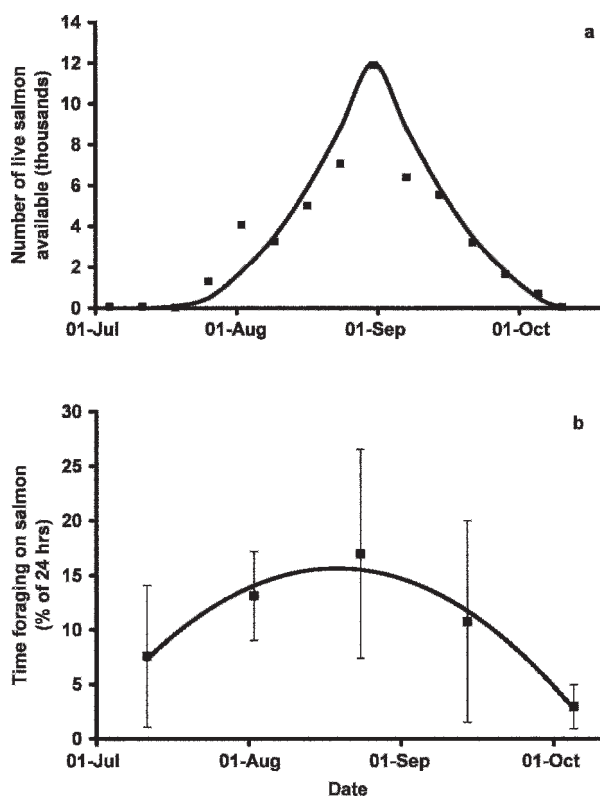


Fig. 2. (a) The number of live salmon in Glacier Creek, Alaska during 2003 and 2004. Line fitted by eye. (b) Time spent by GPS-collared, adult female brown bears in or immediately adjacent to Glacier Creek or Seepage Creek, Alaska in 2002–04.

(SD = 27%) by early October ( $t = -3.55$ ,  $P < 0.01$ ). Collared, adult female brown bears weighed 141 kg (SD = 21; fat = 12.0, SD = 2.8%) in spring and 239 kg (SD = 20 fat = 31.1, SD = 1.7%) in fall.

Brown bears had a significant marine dietary component based on hair isotopic signatures

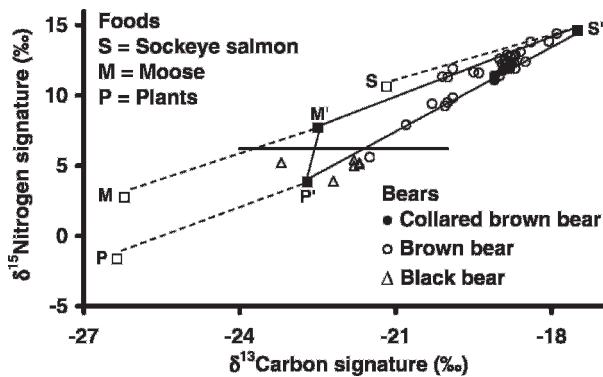
(Fig. 3). There were no significant differences between the isotopic signatures of brown bear hair snared from July through September and fully-grown hair collected in either May or October from the collared bears ( $\delta^{13}\text{C}$ ,  $F = 0.94$ ,  $P = 0.34$ ;  $\delta^{15}\text{N}$ ,  $F = 0.03$ ,  $P = 0.85$ ). There were no significant differences between years in the isotopic signatures or assimilated diets of the 4 adult female brown bears captured all 3 years (salmon,  $F = 0.11$ ,  $P = 0.49$ ; terrestrial meat,  $F = 0.36$ ,  $P = 0.71$ ; plant matter,  $F = 0.69$ ,  $P = 0.53$ ). Similarly, there were no significant differences between years in the isotopic signatures or assimilated diets estimated within each species for samples collected from hair snares ( $\delta^{13}\text{C}$ ,  $F = 1.55$ ,  $P = 0.23$ ;  $\delta^{15}\text{N}$ ,  $F = 2.16$ ,  $P = 0.14$ ).

Mean brown bear isotopic signatures were  $-19.3\text{‰}$  ( $\delta^{13}\text{C}$ ; SD = 0.8) and  $11.5\text{‰}$  ( $\delta^{15}\text{N}$ ; SD = 1.8) and for black bears  $-21.6\text{‰}$  ( $\delta^{13}\text{C}$ ; SD = 1.4) and  $6.0\text{‰}$  ( $\delta^{15}\text{N}$ ; SD = 2.9). The corresponding assimilated diet estimates for brown bears were 66.0% salmon (SD = 16.7) and 20.1% plant matter (SD = 17.2) and for black bears 8.0% salmon (SD = 5.4) and 83.6% plant matter (SD = 7.7) (salmon,  $F = 56.29$ ,  $P < 0.01$ ; plant matter,  $F = 58.94$ ,  $P < 0.01$ ). The dietary proportion of assimilated terrestrial animal matter was 13.9% (SD = 7.5) for brown bears and 8.4% (SD = 9.7) for black bears ( $F = 2.74$ ,  $P = 0.11$ ). Male and female brown bears did not differ in either the proportion of dietary salmon (62.1%, SD = 16.9 and 68.4%, SD = 16.5;  $F = 0.35$ ,  $P = 0.56$ ), terrestrial meat (16.7%, SD = 9.9 and 11.8%, SD = 4.4;  $F = 1.38$ ,  $P = 0.25$ ), or plant matter (21.1%, SD = 17.4 and 19.8%, SD = 17.4,  $F = 0.01$ ,  $P = 0.94$ ). Fecal residues of both species were not significantly different and were heavily weighted toward plant matter, particularly fruit (brown bears: fruit = 87.0%, SD = 15.2, herbage = 12.2%, SD = 13.7; black bears: fruit 91.8%, SD = 7.2, herbage =

Table 1. Nutritional analyses of salmon and major fruits collected on the Kenai Peninsula, Alaska, USA, 2002–04. Fruit analyses include the seeds, which may not be digestible. See Welch et al. (1997) for analyses without seeds.

Food	Dry matter % (SD)	Crude protein % dry matter (SD)	Gross energy kcal/g dry matter (SD)	Digestible Dry Matter, (SD)
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)





**Fig. 3.** Isotopic signatures for bear hair samples collected during capture or on hair-snares along Glacier Creek and Seepage Creek, Kenai Peninsula, Alaska, 2002–04. Mean isotopic signatures are 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  $\delta^{15}\text{N}$ , below which there is <10% contribution from salmon (Ben-David et al. 2004).

7.3%, SD = 6.1) (fruit:  $t = 0.058$ ,  $P = 0.81$ ; herbage  $t = 0.32$ ,  $P = 0.57$ ).

## Discussion

The assimilated diet estimates for salmon use by sympatric brown bears (66.0%, SD = 16.7) and black bears (8.0%, SD = 5.4) on the Kenai Peninsula in the current study are similar to earlier estimates of Jacoby et al. (1999) and Hilderbrand et al. (1999) (50%, SD = 33% and 62%, SD = 24% for brown bears and 0%, SD = 0% for black bears). Thus, although 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 and black bears at Wolverine Cove and Creek on the Alaska Peninsula, black bears moved through the area very quickly and captured <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 and Seepage Creeks is identical to a study in which foot snares were used to capture bears along these creeks. Ten male black bears, 6–10 yrs old and weighing ~100 kg, and no females were captured (Farley, unpublished). Thus, even though the Kenai Peninsula has brown bear densities one-tenth that of black bears, the presence of brown

bears on salmon streams is sufficient to virtually eliminate use of salmon by black bears.

The almost complete absence of salmon in the assimilated diets of black bears leads to their being largely herbivorous and frugivorous (83.6% plant matter, SD = 7.7) as compared to the largely carnivorous brown bears (79.9% animal matter, SD = 17.2). These differences would not have been apparent with fecal analyses because fruits and herbage accounted for >99% of the fecal matter in both species. Because the assimilated diets of black bears determined in this study were only for those male bears that visited a salmon stream, the reliance of black bears on plant matter within the larger population 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.

Brown bear use of salmon in this ecosystem was similar to many other ecosystems with abundant salmon (Gende et al. 2001, Gende and Quinn 2004, Mowat and Heard 2006). Although both male and female brown bears had similar dietary concentrations in our study, adult males can dominate salmon resources in the absence of hunting, when salmon capture rates are high and when fishing sites are limited (Gende and Quinn 2004, Rode et al. 2006). The dietary content of salmon can increase in subordinate brown and black bears when more dominant brown bears are either more limited in number than on the Kenai Peninsula or when brown bears perceive a greater risk from humans than black bears and thereby avoid sites near bear viewers or fishermen (MacHutchon et al. 1998, Chi 1999, Jacoby et al. 1999, Nevin and Gilbert 2005).

In summary, the almost exclusive use of salmon by brown bears when sympatric with black bears is presumably due to (1) the dominance of brown bears over black bears (Mattson et al. 2005), (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 (such as fruits) of a quantity and quality sufficient to meet their needs (Welch et al. 1997). However, adult female brown bears with dependent young may temporarily avoid streams dominated by adult males because of the risk of infanticide (Ben-David et al. 2004).

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USA.

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