Using stable isotopes to understand the feeding ecology of the Hokkaido brown bear (*Ursus arctos*) in Japan

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Abstract: Interactions between brown bears (*Ursus arctos*) and anadromous salmon (*Oncorhynchus* spp.) constitute a unique energy pathway that facilitates nutrient cycling between marine and terrestrial ecosystems. Previous studies have documented variation in salmon consumption by brown bears; however, few have addressed potential anthropogenic factors influencing consumption. We assessed diet of brown bears on Hokkaido Island, Japan, using carbon and nitrogen stable isotopes to determine the effect of demographic (age and sex) and environmental (developed and undeveloped area) factors on salmon consumption. We collected thigh bones from 190 harvested bears from 1996 to 2011 and samples of their major dietary foods from 2009 to 2011, and we then estimated the potential contributions of these foods to the diets of brown bears using a Bayesian mixing model. Brown bears consumed more herbs, fruits, and corn than terrestrial animals or salmon at the population level. However, the dietary contribution of salmon varied widely among bears; in some cases, it comprised >30% of the total diet. Salmon consumption also varied by bear age class, sex, and location. Low salmon consumption by adult females with cubs suggested avoidance of salmon-spawning areas to minimize risk to their cubs. Bears inhabiting undeveloped areas were more likely to consume salmon than those inhabiting developed areas, suggesting that human activities restrict brown bears' salmon consumption. The lower salmon intake of Hokkaido brown bears compared with Alaskan brown bears may be attributed in part to extensive human development on Hokkaido Island, including in-stream structures that preclude salmon migrations and agricultural crops that provide an alternative food subsidy.

Key words: brown bear, development, diet, salmon, stable isotopes, *Ursus arctos*

Brown bears (*Ursus arctos*), which are distributed widely throughout the northern hemisphere, contribute to the transportation of marine-derived nutrients to terrestrial ecosystems by eating anadromous salmon (e.g., Hilderbrand et al. 1999b, Quinn et al. 2009). The salmon–bear interactions provide nutrient cycling across ecosystem boundaries, and therefore this interaction is often called a "keystone interaction" (Helfield and Naiman 2006:168). Marine-derived nutrients imported by brown bears alter nitrogen cycling in riparian soils (Holtgrieve et al. 2009), supplying nutrients to riparian vegetation (Hilderbrand et al. 1999b, Gende and Quinn 2006).

Additionally, salmon is important for the population persistence of brown bears (McLellan 1994, Hilderbrand et al. 1999a). The dietary contribution of salmon to brown bears can affect population density (McLellan 1994, Hilderbrand et al. 1999a) and body size (McLellan 1994, Hilderbrand et al. 1999a, Mowat and Heard 2006).

Studies on bear and salmon interactions in the Pacific coast of North America revealed that brown bears consume large amounts of salmon where this resource is available (e.g., Gende and Quinn 2006, Mowat and Heard 2006), and there are substantial individual differences in salmon use by brown bears even within populations with access to salmon (Mowat and Heard 2006). Knowing how individual

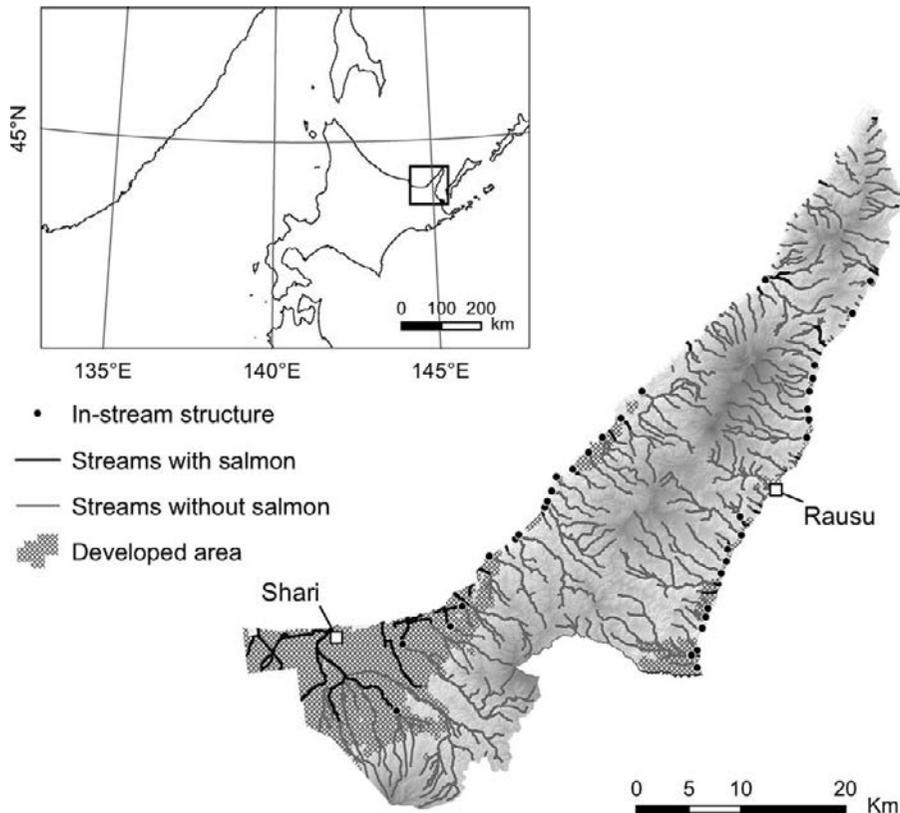[5]email: matsu-jun@ecology.kyoto-u.ac.jp

Fig. 1. Location of study area in Hokkaido Island, Japan, where we assessed diet of brown bears. Developed areas include urban areas and cultivated fields in 2013.

differences in salmon consumption occur is important for understanding the mechanisms of marine-derived nutrient transportation via the salmon–bear interaction.

However, few studies have focused on individual differences in salmon use by brown bears. One such study suggested that social dominance of brown bears is relatively important in determining salmon consumption by individual bears (Gende and Quinn 2004). Additionally, salmon–bear interactions can be limited by human activities. For example, studies in Alaska, USA, suggested that humans strongly influence the daily and seasonal activities of brown bears along salmon-spawning streams (Olson et al. 1997, 1998), and bears avoid using salmon streams where people are frequently found (Olson and Gilbert 1994).

We determined how salmon consumption by brown bears differs between age and sex groups of bears and between developed and undeveloped areas in the Shiretoko Peninsula, Hokkaido Islands, Japan.

Salmon use by brown bears was estimated using stable isotope analysis (SIA), which can quantify the contribution of each diet item to the consumer's diet. We used stable carbon and nitrogen isotopes found in bone collagen, which provide dietary information over several years or the lifespan of the individual (Stenhouse and Baxter 1976, Hedges et al. 2007). The distal area of the Shiretoko Region has been set aside as a nature refuge and is relatively less developed (Nakamura and Komiyama 2010). In contrast, most of the proximal area of Shiretoko has been heavily developed, and therefore we can examine the impact of both demographic (age and sex) and environmental (developed and undeveloped area) factors on salmon use by Hokkaido brown bears.

Study area

This study was undertaken in the Shiretoko Region of Hokkaido Island (43°45′N–44°20′N, 144°33′E–145°21′E; Fig. 1). This region includes

the towns of Shari and Rausu. The mean annual temperature at Shari is 6.0°C with minimum and maximum temperatures of −10.4°C in February and 24.4°C in August, respectively. Mean annual precipitation is 779 mm, with highest and lowest monthly rainfalls of 129 mm in September and 53 mm in February (Japan Meteorological Agency 2013). The Shiretoko Region comprises 1,135 km^2 and its human population is 18,930 (Ministry of Internal Affairs and Communications 2013). The entire region is considered brown bear habitat. Human–bear conflicts are common, and the mean annual bear harvest in this region from 1985 to 2004 was 12.9 bears (Kohira et al. 2009). The major salmon species spawning in the region are chum salmon (*Oncorhynchus keta,* run size: 400–600 mm) and pink salmon (*O. gorbuscha,* run size: 700–800 mm). Of the 44 streams within the Shiretoko Region, 14 have one or more in-stream structure(s) (123 total structures; Nakamura and Komiyama 2010). We defined ''in-stream structure'' as any channel-crossing artificial structure built in a stream, such as check dams and weirs for catching salmon (Nakamura and Komiyama 2010). The maximum elevation of salmon-spawning streams in this region (93.4 m above sea level; Miyakoshi et al. 2011) was set as the upper limit of the salmon run for all major streams shown on the 1:25,000 topographic maps of the area (Fig. 1). When a check dam, or other facility that interrupts salmon runs, was present downstream of this upper limit, we set the limit at the site of said facility.

Methods
Sample collection
From 1991 through 2011, Hokkaido Institute of Environmental Sciences has collected the thighbones of 154 bears killed as nuisance animals, 34 killed for sport hunting, 1 killed in a traffic accident, and 1 that died naturally. The age, sex, location, and cause of death were recorded for each animal. The age of each bear was determined by counting cementum annuli from an extracted tooth (Mundy and Fuller 1964).

We performed SIA for all food types constituting >5% by volume of a bear's stomach contents as measured by Sato et al. (2005), except for leaves and twigs, which are largely indigestible. Because salmon was our primary interest, we included salmon in SIA regardless of its dietary contribution.

We collected samples of C_3 herbs, C_3 fruits, corn, deer (*Cervus nippon*), ants (*Camponotus obscuripes,*

Lasius japonicus, Formica yessensis), and salmon from 4 locations with altitudes ranging from 200 m to 750 m in the Shiretoko Region between July 2009 and October 2011 (Table 1). We pooled fruits, acorns, and nuts into a single group. We used corn as an indicator for agricultural crops because bears frequently feed on corn in Eastern Hokkaido (Sato et al. 2005, Narita et al. 2011).

Sample preparation and isotope analysis
We dried deer and salmon tissues at 60°C for ≥48 hours, and then powdered the tissues in a mortar. To extract the lipids, we placed samples in glass centrifuge tubes and immersed them in a 1:1 solvent of methanol and chloroform. We then mixed samples for 30 seconds, allowed samples to settle for >1 hour, and then centrifuged samples for 10 minutes at 2,500 revolutions/minute. We repeated this process 3 times. We also dried plant tissues and ants at 60°C for >2 days. Lipids were not extracted from these organisms because they generally have extremely low lipid content. Instead, we powdered plant and ant samples in a mortar, and then placed each in tin capsules for elemental and stable isotope analyses. We powdered bear thigh bones using an electric drill and extracted collagen following the methods of Schoeninger and DeNiro (1984), and we used approximately 0.4 mg of extracted collagen from each sample for analyses.

We expressed carbon and nitrogen isotope ratios in δ notation based on the international standard scale, as follows:

$$\delta X(‰) = \left[\left(R_{sample} / R_{standard} \right) - 1 \right] \times 10^3,$$

where X is ^{13}C or ^{15}N, R_{sample} corresponds to the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio of the measured samples, and $R_{standard}$ is the $^{13}C/^{12}C$ of Pee Dee Belemnite (Craig 1957) or the $^{15}N/^{14}N$ of atmospheric nitrogen (Mariotti 1983).

We measured carbon and nitrogen stable isotope ratios using a Finnigan MAT 252 mass spectrometer (Finnigan MAT, Bremen, Germany) connected to a Fisons NA1500 elemental analyzer. For calibration, a proline working standard (Minagawa 1992) was analyzed between every 5 collagen samples. The overall estimated measurement error was <0.1‰ for $\delta^{13}C$ and <0.2‰ for $\delta^{15}N$. Adipose tissues have extremely low $\delta^{13}C$ value compared with protein (DeNiro and Epstein 1978). Our ant samples without lipid extraction showed similar $\delta^{13}C$ value to those of

Table 1. Mean (±SD) stable isotope values for potential brown bear foods, collected between July 2009 and October 2011 in Hokkaido Island, Japan.

Food resources	N	%C	%N	δ¹³C(‰)	δ¹⁵N(‰)
C$_3$ herbs					
Japanese sweet coltsfoot (*Petasites japonicas;* buds)	6	44.9 ± 2.0	2.8 ± 0.2	−28.9 ± 1.1	−2.7 ± 1.3
Japanese sweet coltsfoot (*Petasites japonicas;* stems)	8	31.5 ± 2.2	0.7 ± 0.2	−29.1 ± 0.9	−1.5 ± 2.1
Ezo nettle (*Urtica platyphylla*)	10	38.0 ± 1.6	5.6 ± 2.1	−29.2 ± 1.3	−5.2 ± 1.6
Ezo-kurokumosou (*Saxifraga fusca*)	5	39.2 ± 1.6	2.6 ± 0.7	−30.7 ± 0.8	−3.8 ± 0.7
Ezono-yoroigusa (*Angelica anomala*)	12	41.8 ± 0.8	3.2 ± 1.0	−29.3 ± 1.0	−4.1 ± 2.2
Oo-kasamochi (*Pleurospermum uralense*)	2	42.1 ± 0.0	2.2 ± 0.1	−28.6 ± 0.3	−4.6 ± 0.5
Kneeling angelica (*Angelica genuflexa*)	3	40.1 ± 0.8	2.8 ± 0.4	−30.3 ± 2.2	−2.9 ± 3.8
Sweet cow parsnip (*Heracleum dulce*)	8	39.3 ± 3.5	3.3 ± 1.2	−30.0 ± 0.8	−3.9 ± 1.8
False snowparsley (*Tilingia ajanensis*)	6	41.2 ± 0.8	2.5 ± 0.5	−29.4 ± 0.4	−5.0 ± 1.5
Kawara-boufuu (*Peucedanum terebinthaceum*)	3	42.4 ± 1.5	2.7 ± 1.3	−29.6 ± 1.0	−3.7 ± 0.5
Mitsuba (*Cryptotaenia japonica*)	3	40.5 ± 1.3	2.8 ± 0.5	−32.4 ± 0.2	−2.4 ± 1.1
Umano-mitsuba (*Sanicula chinensis*)	1	39.4	2.7	−33.2	−2.9
C$_3$ fruits					
Mizu-nara (*Quercus mongolica* var. *crispula*)	5	42.0 ± 0.6	1.1 ± 0.2	−27.7 ± 1.0	−1.7 ± 1.0
Crimson glory vine (*Vitis coignetiae*)	6	44.5 ± 1.2	1.2 ± 0.1	−28.6 ± 1.2	−2.0 ± 1.2
Shiuri-zakura (*Padus ssiori*)	2	43.0 ± 0.6	1.7 ± 0.0	−32.6 ± 0.9	−2.1 ± 0.0
Bower actinidia (*Actinidia arguta*)	6	38.3 ± 7.7	1.5 ± 0.4	−30.1 ± 1.1	−1.8 ± 1.2
Udo (*Aralia cordata*)	5	49.4 ± 2.3	1.5 ± 0.2	−29.6 ± 1.9	−2.6 ± 2.0
Corn (*Zea mays*)	10	40.8 ± 2.2	2.9 ± 1.0	−10.9 ± 0.4	−2.3 ± 1.4
Deer					
Sika deer (*Cervus nippon yesoensis*)	10	45.4 ± 1.2	14.1 ± 0.6	−26.4 ± 0.3	4.3 ± 1.1
Ants					
Muneaka-oo-ari (*Camponotus obscuripes*)	2	44.3 ± 0.5	11.0 ± 0.5	−25.7 ± 0.4	1.6 ± 1.2
Tobiiro-ke-ari (*Lasius japonicus*)	1	44.3	11.1	−26.4	0.2
Ezo-akayama-ari (*Formica yessensis*)	7	44.0 ± 1.6	10.0 ± 1.7	−26.3 ± 0.7	4.0 ± 0.9
Salmon					
Pink salmon (*Oncorhynchus gorbuscha*)	11	47.0 ± 1.6	14.9 ± 0.5	−21.1 ± 0.6	10.8 ± 0.7
Chum salmon (*Oncorhynchus keta*)	5	49.0 ± 1.0	15.6 ± 0.3	−20.1 ± 0.6	11.7 ± 0.8

the deer samples with lipid extraction (Table 1), which indicates that our ant samples have low lipid content and their isotopic values were likely not affected by δ¹³C values of adipose tissue.

We assigned male and female bears to 3 age categories: dependent young (1–2 yr old), subadults (3–4 yr old, no longer with their mothers but not yet mature), and adults (>4 yr old, the age at which females begin breeding; Mano and Tsubota 2002; Table 2). We excluded bears <1 year old because nursing would influence the nitrogen isotope signature (Hobson et al. 2000, Polischuk et al. 2001).

Statistical analysis and mixing model

We first employed a K nearest-neighbors randomization test with the Bonferroni *P*-adjustment method ($P < 0.003$; Schilling 1986, Rosing et al. 1998) to investigate whether the stable isotope ratios of the various food types differed from each other. Groups that did not show significant differences were

combined. We then evaluated the proportional contribution of each food resource to the diets of individual bears using a Bayesian isotopic mixing model (Parnell et al. 2010) available in Program R, Stable Isotope Analysis in R (SIAR). The SIAR model was fitted using a Markov chain Monte Carlo procedure to simulate plausible values for the dietary proportion of each source consistent with the data, based on a Dirichlet prior distribution (Jackson et al. 2009, Parnell et al. 2010). We ran the SIAR Markov chain Monte Carlo procedure for 1,000,000 iterations with a thinning period of 15 cycles, and we discarded the first 100,000 iterations to avoid possible effects of the starting value. We assigned an elemental concentration (e.g., % C and % N; Phillips and Koch 2002) and standard deviation (SD) for each parameter of the model. Because different tissues incorporate isotopes at different rates (Reich et al. 2008), we applied a correction factor for bone collagen to incorporate the isotopic discrimination between

Table 2. Mean (±SD) stable isotope values from bone collagen of brown bears killed in Hokkaido Island, Japan, 1996–2011.

Sex–age class	N	%C	%N	δ^{13}C(‰)	δ^{15}N(‰)
Males					
1–2 yr (dependent young)	49	42.0 ± 2.53	15.1 ± 0.87	−21.2 ± 1.15	4.2 ± 2.43
3–4 yr (subad)	27	42.2 ± 2.08	15.3 ± 0.74	−20.5 ± 1.33	5.7 ± 2.61
>4 yr (ad)	32	41.8 ± 2.87	15.0 ± 1.00	−21.0 ± 1.21	4.8 ± 2.14
Females					
1–2 yr (dependent young)	34	43.2 ± 1.19	15.5 ± 0.54	−21.8 ± 0.58	2.9 ± 1.63
3–4 yr (subad)	20	42.4 ± 1.74	15.2 ± 0.54	−21.0 ± 0.72	4.8 ± 2.03
>4 yr (ad)	28	42.9 ± 2.56	15.4 ± 0.88	−21.2 ± 0.89	2.9 ± 2.48

consumer and prey before generating the model. We used a fractionation of 5.0‰ (Vogel 1978, von Schirnding et al. 1982, Schoeninger and DeNiro 1984, Lee-Thorp et al. 1989) ± 1.5‰ SD (Hedges 2003) for δ^{13}C and 3.0‰ ± 1.5‰ SD for δ^{15}N (DeNiro and Epstein 1981, Minagawa and Wada 1984, Schoeninger and DeNiro 1984, Ambrose and DeNiro 1986, Sealy et al. 1987).

The resulting probability–density function distributions of the feasible foraging solutions produced by SIAR allowed direct identification of the most probable solution (i.e., the median value; Jackson et al. 2009, Parnell et al. 2010). Consequently, we compared the median contribution of salmon to the assimilated diets of individual bears among age and sex classes. The differences between sexes were tested within age classes (e.g., dependent young males vs. dependent young females), and the differences between age groups were tested within sexes (e.g., dependent young males vs. subadult males) using the non-parametric Kruskal–Wallis test followed by the Steel–Dwass multiple-comparisons tests. To assess the effect of habitat quality, we defined the area north of the upper limit of human development in this region (Fig. 1) as "undeveloped" and the remaining area as "developed." Then, we compared assimilated salmon between bears in developed area versus undeveloped area. The differences between undeveloped and developed areas were tested using a Wilcoxon test ($P < 0.050$).

Results
Stable isotope ratios

Stable isotope values (δ^{13}C and δ^{15}N) differed among C_3 herbs, C_3 fruits, crops, and salmon (K nearest-neighbor test; $P < 0.005$). Deer and ants had similar isotopic values ($P > 0.500$) and were grouped

as terrestrial animals (Table 3). Stable isotope ratios of the bone-collagen samples from bears were highly variable (−23.59‰ to −17.84‰ for δ^{13}C and −0.78‰ to 11.14‰ for δ^{15}N; Table 2; Fig. 2). Thirty-five of the 191 bears may have consumed salmon because their isotopic values were similar enough to that of salmon to assume consumption of salmon (see Fig. 2).

Dietary proportions of individual bears estimated by SIAR

Median estimated percentage of assimilated diet was 32% for C_3 herbs (SD = 7, range = 6–56%), 29% for C_3 fruits (SD = 3, range = 21–35%), 15% for terrestrial animals (SD = 10, range = 1–29%), 12% for corn (SD = 5, range = 1–21%), and 5% for salmon (SD = 7, range = 0–32%). There were significant differences in the proportions of salmon among the age and sex groups of bears ($W = 1,525$, 5 df, $P < 0.050$, Kruskal–Wallis test). An age-related difference in salmon consumption was found for dependent young (2%) versus subadult females (6%; Table 4). Sex-related differences in salmon consumption were found in dependent young bears (with males consuming 5% salmon and females consuming 2% salmon) and in adult bears (with males consuming 6% salmon and females consuming 3% salmon; Table 4). Among the sex and age classes, subadult males consumed the largest amount of salmon (10%), while dependent young females consumed the least (2%; Table 4). Out of 190 bears, salmon accounted for >10% of the assimilated diet of 28 bears and >20% of the assimilated diet of 13 bears. The dietary proportion of salmon was greater in the undeveloped area north of 44.1°N than in the developed area ($W = 2,611$, $P < 0.050$; Fig. 3; Table 4). Fourteen of 32 bears from the northern area had diets of >10% salmon, and 5 of these bears

Table 3. Mean (±SD) stable isotope values for potential brown bear prey groups, Hokkaido Island, Japan, 2009–2011.

Food items	N	%C	%N	$\delta^{13}C(‰)$	$\delta^{15}N(‰)$
C₃ herbs	67	39.6 ± 4.0	3.0 ± 1.7	−29.7 ± 1.4	−3.7 ± 2.1
C₃ fruits	24	43.3 ± 5.6	1.4 ± 0.3	−29.3 ± 1.8	−2.0 ± 1.4
Corn	10	40.8 ± 2.2	2.9 ± 1.0	−10.9 ± 0.4	−2.3 ± 1.4
Terrestrial animals	20	44.8 ± 1.4	12.2 ± 2.2	−26.3 ± 0.5	3.7 ± 1.5
Salmon	16	47.6 ± 1.7	15.1 ± 0.5	−20.8 ± 0.8	11.1 ± 0.9

consumed >20% salmon. Fifteen of 129 bears from the southern area had diets of >10% salmon, and 8 of these bears consumed >20% salmon. Precise location data for the remaining 29 bears were not available.

Discussion

Differences in salmon consumption among demographic groups may be due to avoidance of salmon-spawning areas by females with cubs. Males tend to congregate at salmon-spawning areas, increasing the risk of infanticide (Ben-David et al. 2004). Therefore, we expect that females with cubs avoid salmon streams to minimize the risk of infanticide by males. Recent studies have suggested that infanticide drives differences in habitat use (Dahle and Swenson 2003,

Ben-David et al. 2004, Rode et al. 2006). Lower salmon consumption by adult females compared with adult males can be attributed to this nurturing-related factor. Additionally, the presence or absence of adult males appears to play a role in determining habitat use by other sex and age classes, particularly females with cubs (Ben-David et al. 2004). In contrast to adult females with cubs, subadult females should be able to use salmon freely because they are sexually immature and independent from their mothers, and therefore their salmon consumption would be higher than for dependent young females. However, our data did not show differences in salmon consumption between subadult and adult females. Differences between the inter-birth interval (2.3–3.0 yr) and the period of association with cubs (1.25–2.25 yr) indicated that adult females are
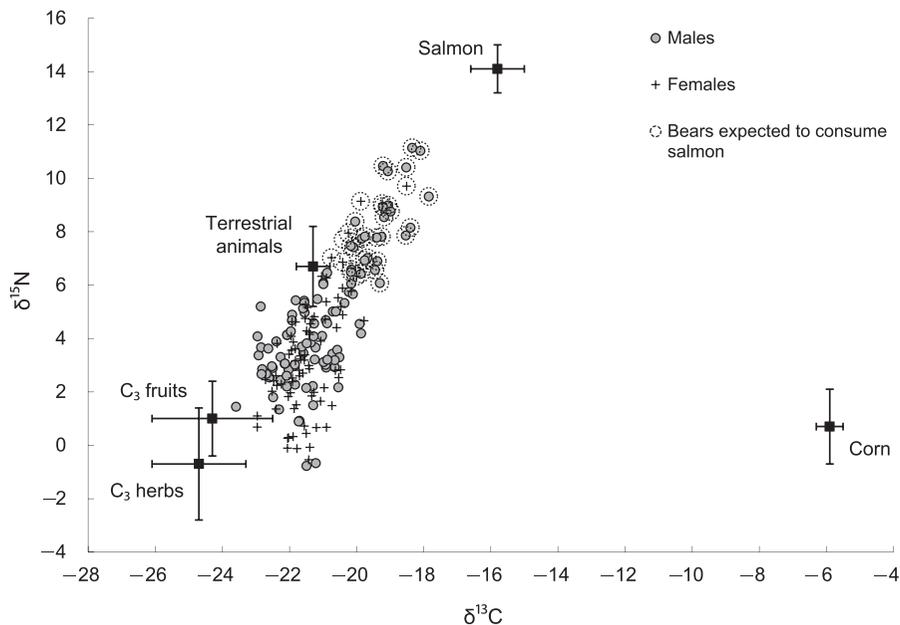

Fig. 2. Mean (±SD) carbon and nitrogen stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) from bone collagen of brown bears and prey groups after correcting for fractionation, Hokkaido Island, Japan, 1996–2011. Bears from locations with a dashed circle consumed salmon based on isotopic endpoints.

Table 4. Mean (±SD) percentage assimilated diet of brown bears killed in Hokkaido Island, Japan, 1996–2011. The median proportion of each dietary item estimated using a Bayesian mixing model was averaged for each group.

Sex–age class	N	C$_3$ herbs	C$_3$ fruits	Corn	Terrestrial animals	Salmon
Males						
1–2 yr (dependent young)	49	33 ± 7[a,b,c]	29 ± 3[a,b]	12 ± 4[a,b]	15 ± 10	5 ± 8[a,c]
3–4 yr (subad)	27	28 ± 7[a]	27 ± 3[a]	13 ± 4[a]	19 ± 9	10 ± 10[a]
>4 yr (ad)	32	31 ± 5[a,d]	29 ± 3[a,b]	12 ± 5[a,b]	17 ± 9	6 ± 7[a]
Females						
1–2 yr (dependent young)	34	36 ± 5[b,c]	31 ± 2[b]	10 ± 3[b]	10 ± 10	2 ± 2[b]
3–4 yr (subad)	20	31 ± 5[a,b]	29 ± 3[a]	12 ± 3[a,b]	19 ± 10	6 ± 7[a,c]
>4 yr (ad)	28	36 ± 8[c,d]	29 ± 3[a,b]	14 ± 3[a]	12 ± 11	3 ± 5[b,c]
Developed area	129	33 ± 6*	29 ± 3*	12 ± 4*	15 ± 10	4 ± 7*
Undeveloped area	32	29 ± 7	27 ± 3	14 ± 4	18 ± 10	9 ± 9

[a]Means of dietary proportions in the same column followed by the same letter are not significantly different at the 5% level according to the Steel–Dwass' procedure.

*Mean dietary proportions in the same column are significantly different between developed and undeveloped areas at the 5% level according to the Wilcoxon test.

without cubs for 1 out of every 3 years (Mano and Tsubota 2002). Because the behavior of female bears varies by reproductive status (McLoughlin et al. 2002), adult females without dependent young may use salmon in proportions similar to subadult females, which would explain the similarity in isotopic values between adult and subadult females. The difference in salmon consumption between dependent young males and dependent young females is more difficult to explain because they seem to have similar diets. Their difference in salmon consumption may be related to differences in body size. Brown bears exhibit sexual dimorphism in body size (Blanchard 1987, Ohdachi et al. 1992); this suggests that dependent young males may consume greater amounts of salmon to meet greater energetic demands. Reduced use of salmon by females with dependent young may in part be to avoid males and reduce risk of infanticide (Dahle and Swenson 2003, Ben-David et al. 2004, Rode et al. 2006).

Despite the abundance of salmon runs during the spawning season in Shiretoko (Nakamura and Komiyama 2010), the estimated proportion of salmon in assimilated diets of brown bears was relatively low. In contrast, bears from coastal areas of North America often obtain >30% of their annual assimilated diets from salmon (Hilderbrand et al. 1996, Mowat and Heard 2006). Even in areas where salmon are available far from coastal areas, salmon consumption is much greater in Alaska (Belant et al. 2006). The lower contribution of salmon to the diet of Hokkaido brown bears is consistent with previous studies of population-level salmon consumption by these bears (Ohdachi and Aoi 1987, Sato et al. 2005). Such a low rate of salmon use has not been reported previously for brown bear populations of the Pacific Rim with access to salmon. Lower salmon consumption in developed areas in our study suggests that development of coastal areas, including in-stream structures such as dams and weirs, may restrict salmon consumption by bears. Bears tend to avoid human-modified areas (Davis et al. 2006) and also may have avoided coastal locations in our study, where salmon congregate before migration. Numerous in-stream structures in Shiretoko potentially may limit salmon consumption by brown bears by preventing salmon from migrating upstream (Nakamura and Komiyama 2010). Also, agricultural crops may be an alternative food to salmon resources, which would decrease the relative importance of salmon to bear diets.

There are ≥3 sources of sampling bias in our study. First, our data included bears killed by sport hunters and because of nuisance behavior, and these differences in sampling may have influenced our conclusions. For example, greater δ^{15}N values from the hair of nuisance brown bears than from research bears has been reported (Hobson et al. 2000), because nuisance bears tend to seek human-related high-quality food. However, the long timeframe of the dietary information provided by the stable isotope values of bone collagen may decrease differences in diet between nuisance and hunter-killed bears. In addition, because nuisance bears are killed immediately after exhibiting problematic behavior in Shiretoko, we suggest that the stable isotope ratios of
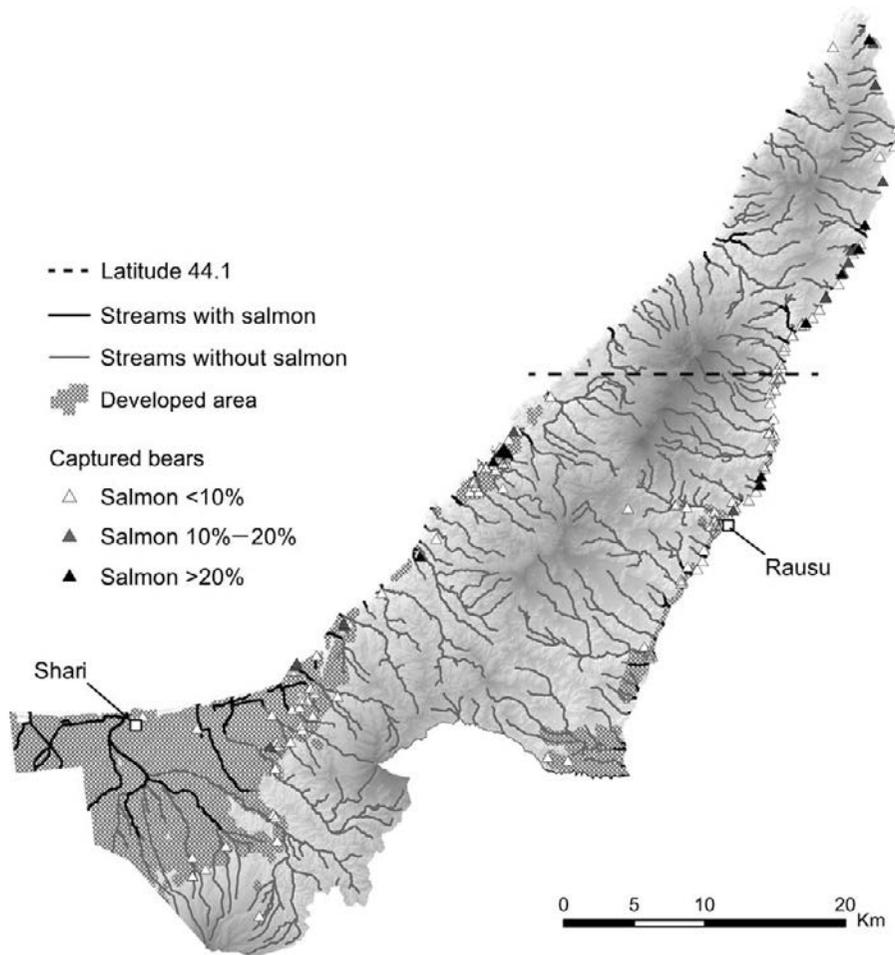
Fig. 3.   Capture locations and percentage of salmon in brown bear diets, Hokkaido Island, Japan, 1996–2011. Latitude 44.1 marks the upper limit of developed areas.

bone collagen of these bears predominantly reflect their dietary habits before the nuisance activity. The second source of bias is that our sample was largely from coastal areas, with few sampled bears from alpine areas. Culling of nuisance bears only occurs near human areas such as agricultural lands, urban areas, and fishermen's barns, which occur exclusively in coastal areas. However, because we focused on salmon–bear interactions, the lack of alpine bears (which most likely consume few or no salmon) should not strongly influence our conclusions. Finally, our SIA results may underestimate total consumption of crops. We used corn as an indicator of agricultural crops; Sato et al. (2005) reported that corn accounted for 62% of crops eaten by bears in eastern Hokkaido.

Management implications

The late-summer diet of bears in the Shiretoko Region includes fruits, nuts, agricultural crops, and salmon. Among these food resources, nuts and fruits vary in abundance between years. When fruit and nut abundance is low and salmon availability is restricted by coastal development and in-stream structures, bears may forage more on human crops. Therefore, removal or improvement of in-stream structures may reduce bear–human conflicts by enabling bears to obtain salmon during late summer when terrestrial foods vary in abundance. In particular, the abundance of pink salmon likely has a substantial effect because this salmon species returns to its natal streams from August to October, when most of the natural food resources for

Hokkaido brown bears are scarce (Sato et al. 2004, 2005). Thus, the incidence of nuisance bear behavior may be low in years with large pink salmon runs because the greater salmon availability would decrease the bears' need to search for food in areas of human settlement.

To help ensure that salmon are available for brown bears, practical and effective modifications of in-stream structures are needed. Such improvements have been applied in Shiretoko since 2008 (Nakamura and Komiyama 2010). Removing weirs associated with salmon hatcheries may also be effective because salmon hatcheries are located at streams with abundant salmon, which likely decreases the amount of non-hatchery fish available to brown bears. To improve human–bear coexistence and to conserve valuable ecosystem processes, further studies of methods to restore salmon–bear interactions are needed.

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