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Changes in body condition and behavior
of Hokkaido brown bears in relation to
seasonal and annual variations in diet

(食性の季節変化および年次変動が
ヒグマの栄養状態と行動様式に与える影響の解明)

Yuri Shirane

CHANGES IN BODY CONDITION AND BEHAVIOR
OF HOKKAIDO BROWN BEARS IN RELATION TO
SEASONAL AND ANNUAL VARIATIONS IN DIET

食性の季節変化および年次変動が
ヒグマの栄養状態と行動様式に与える影響の解明

A Dissertation

Presented in Partial Fulfillment of the Requirements for
the Degree of Doctor of Philosophy

By

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SYNOPSIS

Nutrient balance is an important determinant of animal fitness and demography. Brown bears are omnivores that can change their diet opportunistically in response to temporal variation in resources. On the Shiretoko Peninsula, Hokkaido, brown bears have seasonal access to high-lipid foods, Japanese stone pine nuts, and high-protein foods, pink salmon. This study aimed to clarify seasonal and annual variation in the consumption of high-nutrition foods among Shiretoko brown bears, and how those variations affect bear body condition and behavior.

Chapter 1: A noninvasive method that uses photographs was developed to assess the body condition of free-ranging brown bears. The precision of photograph-based measurements was examined using photographs of an identifiable bear in the Rusha area, a special wildlife protection area. As a result, the torso height:horizontal torso length (TH:HTL) was adopted as the best method that could apply to bears with various postures and reflected seasonal changes of body condition. Then, body condition index (BCI) was calculated from actual measurements of captured 7 females and TH:HTL from photographs of the same individuals. The significant positive correlation between TH:HTL and BCI ($r = 0.78$) suggested that the body condition of bears can be estimated with high accuracy.

Chapter 2: To assess seasonal and annual fluctuation in adult female body condition in relation to diet and reproductive status, a longitudinal study was conducted in the Rusha area during 2012–2018. Analyses of 2,079 bear scats revealed that pine nuts in August and salmon in September accounted for 39.8% and 46.1% of energy intake, respectively, with large annual fluctuation. Using the method developed in chapter 1, body condition was evaluated from 1,226 photographs of 12 adult females and found that body condition continued to decline until late August and started to increase in September. In addition, body condition began to recover earlier in years with high pine nuts and salmon consumption. Furthermore, females with offspring had poorer body condition than solitary females.

Chapter 3: GPS data were used to clarify how females changed their behavior depending on reproductive status and diet. Calculation of hourly movement velocities showed that females with offspring moved more slowly than solitary females in early and late summer, especially in the alpine region. There was no significant difference in the probability of visiting salmon spawning sites with or without offspring. In addition, bears strongly selected the alpine region in late summer, regardless of reproductive status, while they avoided the alpine region in years with

low pine nut consumption. Female brown bears with cubs were restricted in movement, but do not differ from solitary females in acquiring pine nuts and salmon.

This study revealed that pine nuts and salmon are key foods that determine the body condition and behavior of brown bears on the Shiretoko Peninsula. These findings may help clarify the causes of human–bear conflict in Shiretoko, which may be due to summer food shortages. Further studies investigating differences in diet by age-sex classes and how regional differences in food availability affect bear behavior are required to clarify population dynamics and to inform management and conservation strategies.

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LIST OF ABBREVIATIONS

The following table describes the significance of various abbreviations and acronyms used throughout the thesis. The page on which each one is defined or first used is also given.

Abbreviation	Meaning	Page
AICc	Akaike's information criterion corrected for small sample size	55
ANOVA	Analysis of variance	22
BCI	Body condition index	20
BCS	Body condition score	19
BL	body length	22
“BS”	photographs with a score of 2 for body straightness only	24
CF _D	Correction factors used to calculate EDC	53
CF _E	Correlation factors used to EDEC	53
CV	coefficient of variation	24
EBL	Euclidean straight-line body length	23
EDC	estimated dietary content	53
EDEC	estimated digestible energy content	53
GAMM	generalized additive mixed model	54
“Good”	photographs that had a score of 1 for all attributes	24
GPS	Global Positioning System	78
HBL	horizontal straight-line body length	23
HTL	horizontal straight-line torso length	24
MCP	minimum convex polygon	81
“NB”	photographs with a score of 2 for neck lateral bending only	24
“NF”	photographs with a score of 2 for neck flexing only	24
PBL	polygonal-line body length	24
PDOP	Positional dilution of precision	80
RSF	resource selection function	81
TH	torso height	22
UNESCO	United Nations Educational, Scientific and Cultural Organization	14
vFV	percent volume of each food item estimated visually	52

LIST OF PUBLICATIONS

I. Publication related to the dissertation

- I-I.** Shirane Y, Mori F, Yamanaka M, Nakanishi M, Ishinazaka T, Mano T, Jimbo M, Sashika M, Tsubota T, and Shimozuru M. 2020. Development of a noninvasive photograph-based method for the evaluation of body condition in free-ranging brown bears. *PeerJ* 8: e9982.

II. Reference publication

- II-I.** Shirane Y, Shimozuru M, Yamanaka M, Tsuruga H, Hirano S, Nagano N, Moriwaki J, Nakanishi M, Ishinazaka T, Nose T, Kasai S, Shirayanagi M, Masuda Y, Fujimoto Y, Osada M, Akaishi M, Mano T, Masuda R, Sashika M, and Tsubota T. 2018. Sex-biased natal dispersal in Hokkaido brown bears revealed through mitochondrial DNA analysis. *European Journal of Wildlife Research* 64(6): 65.

- II-II.** Shirane Y*, Shimozuru M*, Yamanaka M, Tsuruga H, Nakanishi M, Ishinazaka T, Nose T, Kasai S, Shirayanagi M, Masuda Y, Fujimoto Y, Mano T, Sashika M, and Tsubota T. 2019. Sex-biased dispersal and inbreeding avoidance in Hokkaido brown bears. *Journal of Mammalogy* 100(4): 1317–1326.

*Authors with equal contribution

The contribution of Y. Shirane to the publications was as follows.

Publication I-I: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding Acquisition (lead); Investigation (equal); Methodology (lead); Validation (equal); Visualization (lead); Writing–Original Draft Preparation (lead).

Publication II-I: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Validation (equal); Visualization (lead); Writing–Original Draft Preparation (lead).

Publication II-II: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Validation (equal); Visualization (lead); Writing–Original Draft Preparation (lead).

NOTES

My first project investigated sex-biased natal dispersal patterns of brown bears in the Shiretoko Peninsula, Hokkaido, Japan. Natal dispersal, defined as the movement of an individual from its birthplace to the location where it will reproduce, plays a major role in the demography and genetic structure of populations. In addition, the dispersal of young bears with insufficient human experience is one of the causes of human-bear conflict. Therefore, understanding natal dispersal patterns is fundamental in the ecology and conservation biology of brown bears. A total of 760 individual samples (e.g., tissue, hair, and scat) were collected throughout the peninsula during 1998–2016, and haplotypes from the mitochondrial DNA control region were analyzed (**Publication II-I**). As a result, the distribution of haplotypes in females was geographically structured, whereas haplotypes in males were distributed widely throughout the peninsula. This finding suggests that the mitochondrial DNA haplotype distribution has been maintained by female philopatry, and that bears exhibit male-biased dispersal. In addition, 837 individuals collected in 1998–2017 were genotyped at 21 microsatellite loci and parentage analysis was performed (**Publication II-II**). Using the site where the mother and offspring were identified, dispersal distances were calculated. The results showed that dispersal distances were significantly greater for males than for females, and that males begin to disperse around the time sexual maturation begins (i.e., at 3 years old). Furthermore, closely related female–male pairs rarely resided in close proximity, suggesting that the potential for close inbreeding was low in Hokkaido brown bears because males are effective dispersers.

My second project focused on changes in body condition and behavior of brown bears in relation to temporal variations in diet. To clarify seasonal and annual changes in the body condition of free-ranging brown bears, the body condition must be repeatedly monitored for several years. To achieve this, a noninvasive method of evaluating the body condition of brown bears based on morphometric measurements obtained from photographs was developed (**Publication I-I**, Chapter 1). Chapter II reports studies that have performed long-term monitoring of the body condition of 12 adult females using the techniques developed in **Publication I-I**. In addition, Chapter 3 explains the results of studies that used GPS data to clarify how females changed their behavior depending on reproductive status and diet.

PREFACE

Studied species

Brown bears (*Ursus arctos*, Fig. 1) are large mammals that are widely distributed throughout the Palearctic (Europe and Asia) and Nearctic (North America) faunal regions. They are sexually dimorphic, adult males being 1.2–2.2 times larger than females (approximately 200–400 kg for males and 100–200 kg for females; Swenson et al. 2007; Moriwaki et al. 2018). The home ranges of adult males are larger than, but often overlapping with, those of females. Male brown bears show a strong tendency to disperse from their natal place, whereas females are usually philopatric and stay near their mothers' home ranges (Blanchard and Knight 1991; Shirane et al. 2018; Støen et al. 2005). Closely related female-male pairs rarely reside in close proximity, indicating that close inbreeding has been effectively avoided due to male-biased dispersal (Costello et al. 2008; Shirane et al. 2019).

Brown bears are usually active from April to October and undergo four annual physiological stages (Nelson et al. 1983): 3–7 months of winter dormancy without eating, drinking, defecating, or urinating (Stage I, hibernation); followed by emergence from the den in the spring with initial low intake of food and water (Stage II, hypophagia); a stage of normal activity in summer (Stage III); and finally, a period of increased food intake in autumn to build up fat reserves for hibernation (Stage IV, hyperphagia).

Brown bears are opportunistic omnivores that can change their diet in response to spatial and seasonal variation in food resources (Bojarska and Selva 2012; Kavčič et al. 2015). They usually eat green vegetation (such as forbs and graminoids) and ants in spring and early summer. During this period, bears also hunt the calves of ungulates such as moose (*Alces alces*) where these are available (Niedziałkowska et al. 2019). In late summer, when the nutritional value of herbaceous plants decreases (Cicnjak et al. 1987) and berries are still immature, diets vary according to habitat. In some populations, bears move to various habitats, such as northern slopes (Rodríguez et al. 2007), creek bottoms (Mealey 1980), or alpine habitats (Munro et al. 2006), looking for premature herbaceous plants. In other populations, bears feed on alternative food items, including fish (Mattson et al. 1991) and anthropogenic foods such as livestock (Piédallu et al. 2016) and crops (Sato et al. 2005). Bears switch to berries and fruits like *Vaccinium* spp. and *Empetrum* spp. when these ripen, and in autumn, they consume large amounts of hard mast such as acorns (*Quercus* spp.) and chestnuts (*Castanea* spp.). Salmon (*Oncorhynchus* spp.) is one of the most important food resources for some populations. Bears in populations with a higher

proportion of salmon in their diets have larger body size and higher reproductive success (Hilderbrand et al. 1999b).

The body mass and condition of brown bears change dynamically with the seasons. During hibernation, lean body mass is preserved and body fat supplies energy. Weight loss during this period depends on the body condition of the bear when entering the den (Atkinson et al. 1996; Atkinson and Ramsay 1995), length of the denning season, and reproductive status (Hilderbrand et al. 2000). The spring, after den emergence, is considered a negative foraging period because the costs of maintenance, growth, and cub rearing (Hilderbrand et al. 2000) lead many wild bears to lose body fat and lean tissue during this period (Blanchard 1987; Eagle and Pelton 1983; Hellgren et al. 1989). However, in some populations that have access to ungulates in the spring, bears maintain or gain mass during this period (Blanchard 1987; Hilderbrand et al. 1999a). In autumn, when bears feed intensively before denning, they gain mass rapidly (Blanchard 1987; Hilderbrand et al. 2000). This pre-denning mass gain is essential for reproduction and survival because bears rely solely on their stored energy reserves during hibernation (Hertel et al. 2018; McLellan 2015). Body mass and condition of bears peak in autumn just prior to hibernation in most populations, although the poorest times vary from spring to late summer, depending on food availability in a given habitat (Hilderbrand et al. 1999a; McLellan 2011; Schwartz et al. 2014).

Brown bears are solitary animals with a promiscuous mating system (Schwartz et al. 2003a; Steyaert et al. 2012). Generally, females reach sexual maturity between 4 and 7 years of age and give birth to 1–3 cubs every 1–4 years (McLellan 1994; Shimozuru et al. 2017; Zedrosser et al. 2011). The mating season of the brown bear lasts for approximately 2.5 months, from late spring to early summer (Craighead et al. 1995; Spady et al. 2007). In a single breeding season, males and females both mate with multiple partners. Multiple paternity within a litter has been reported in several brown bear populations (Bellemain et al. 2006; Shimozuru et al. 2019). Implantation is delayed until late November and females give birth to cubs during the denning period, between January and March (Mano and Tsubota 2002; Schwartz et al. 2003b). Males do not participate in parental care, and mothers and offspring remain together for 1.5 to 4.5 years (Dahle and Swenson 2003a; Shimozuru et al. 2017). Females usually separate from their offspring prior to, or early in the mating season. Although females do not mate until their offspring are weaned, females that lose offspring by either death or family break-up can enter estrus within 2–7 days after the loss (McLellan 2005; Swenson and Haroldson 2008). Therefore, males may obtain more breeding opportunities by killing unrelated young and monitoring the mother until she enters estrus (Hrdy 1979).

Study area and studied population

In Japan, brown bears inhabit only Hokkaido, the northernmost island of the country. The Shiretoko Peninsula (43°50′–44°20′ N, 144°45′–145°20′ E), located in eastern Hokkaido, has one of the highest densities of brown bear populations worldwide (Hokkaido Government 2017). This peninsula protrudes into the Sea of Okhotsk and is a long and narrow peninsula (approximately 70 km × 25 km), with an area of about 1,760 km². An area from the middle to the tip of the peninsula, covering 386 km², has been designated as Shiretoko National Park. In addition, the United Nations Educational, Scientific and Cultural Organization (UNESCO) listed a 711-km² area of this peninsula as a World Natural Heritage Site in July 2005, being valued for its unique ecosystem formed by the interrelationship of its marine and terrestrial environments. The Shiretoko mountain range extends along the central axis of the peninsula, with flat land between the ridgeline and the coasts. These mountains reach 1,500–1,600 m in height within 10 km of the coastline and generate a large number of steep slopes and streams.

The Rusha area (44°12′ N, 145°12′ E; approximately 11.5 km²), which is located near the tip of the peninsula, has been designated as a special wildlife protection area (Fig. 2). This area is a narrow estuarine coast stretching south to north for approximately 3 km. Three streams, where pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) spawn naturally, flow into the sea within the Rusha area (Nakamura and Komiyama 2010). Public access is not allowed in this area without permission and there is no human residence except for one fishermen's settlement. Because the fishermen have not excluded bears from the settlement area in the last few decades, the bears have become habituated to the existence of humans, which enables direct observation at close range (Shimozuru et al. 2020). Long-term visual monitoring of identifiable bears and genetic surveys have been conducted in this region since the late 1990s and since 2008, respectively (Kohira et al. 2009; Shimozuru et al. 2017; Shirane et al. 2018). In a previous study investigating reproductive parameters in the Rusha area, an average of about 40 individuals were observed annually, including 15 adult females and 3 adult males (Shimozuru et al. 2017).

The Shiretoko Peninsula contains high-quality brown bear habitat with a wide variety of food resources ranging from the coastal (*e.g.*, pink salmon) to the alpine regions (*e.g.*, Japanese stone pine, *Pinus pumila*) (Ohdachi and Aoi 1987). However, human–bear conflicts, including agricultural crop depredation and intrusion into human residential areas, have become a serious problem in this peninsula. Since there is no buffer zone between the national park and residential areas, bears can intrude into these areas. Over the past decade, an average of 34 bears have been killed each year, mainly for management purposes (Kohira et al. 2009; Shimozuru et al. 2020). With the aim of mitigating such human–bear conflicts, Brown Bear Conservation and Management Policy in the Shiretoko Peninsula was established in 2012, and Brown Bear

Conservation and Management Plan in Hokkaido was formulated in 2014. However, there is a lack of basic ecological information about brown bears in Hokkaido, such as the relationship between diet, nutritional status, and behavior.

Perspectives

This study aimed to clarify seasonal and annual variation in the consumption of high-nutrition foods among Shiretoko brown bears, and how those variations affect bear body condition and behavior. In **Chapter 1**, a noninvasive method that uses photographs was developed to assess the body condition of free-ranging brown bears. The precision of photograph-based measurements was examined using photographs of an identifiable bear in the Rusha area. In addition, the accuracy of the photograph-based measurement method was validated by using actual measurements of 7 captured individuals. In **Chapter 2**, to assess seasonal and annual fluctuation in adult female body condition in relation to diet and reproductive status, a 7-year longitudinal study was conducted in the Rusha area that included scat sampling and direct observation of bears. Using the method developed in **Chapter 1**, body condition of 12 adult females was evaluated. In **Chapter 3**, GPS data obtained from seven adult female bears were used to clarify how females changed their behavior depending on reproductive status and diet. I tested hypothesis that females with offspring were restricted from obtaining food resources due to poor mobility of cubs.



Figure 1. A brown bear catching salmon.

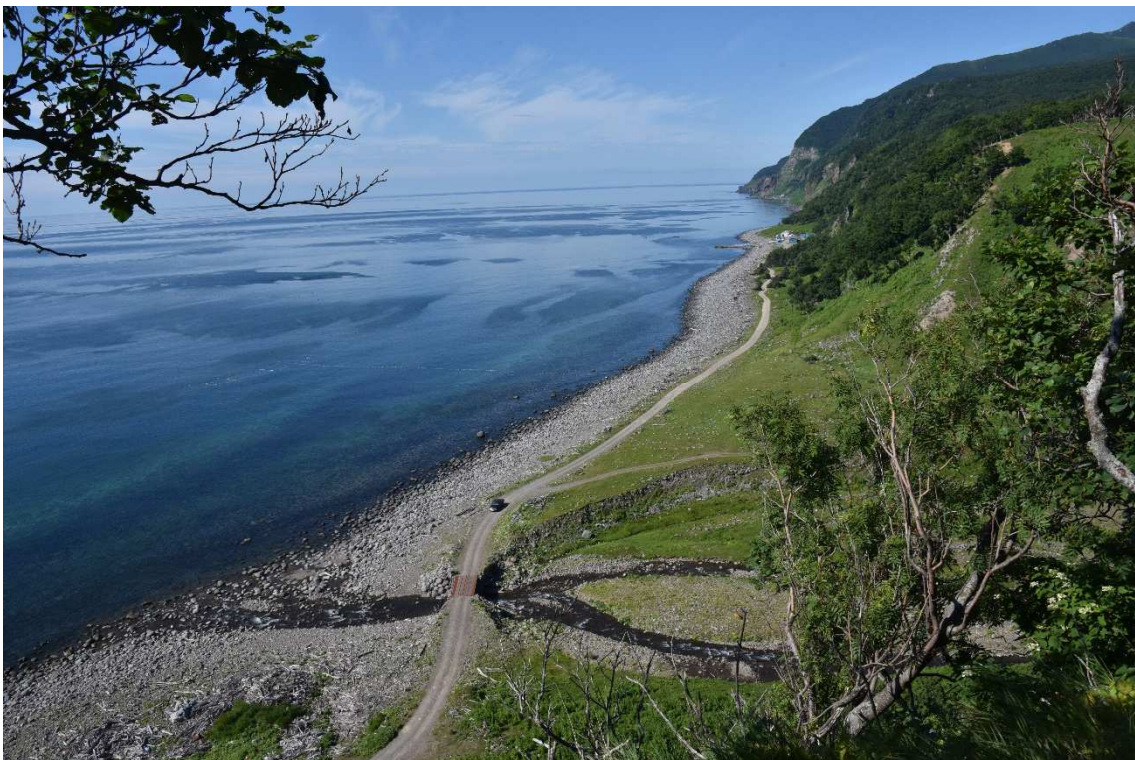


Figure 2. The Rurua area of the Shiretoko Peninsula, Hokkaido, Japan.

CHAPTER 1

Development of a noninvasive photograph-based method for the evaluation of body condition in free-ranging brown bears

INTRODUCTION

Body condition, defined as the energetic state in an individual, especially the relative size of energy reserves such as fat and protein (Gosler 1996; Peig and Green 2009; Schulte-Hostedde et al. 2001), is an important determinant of health in both terrestrial and marine mammals. It serves as an indicator of food quality (Mahoney et al. 2001; McLellan 2011), reproductive success (Guinet et al. 1998; Noyce and Garshelis 1994), and survivorship (Gaillard et al. 2000; Young 1976). Animals in good body condition generally have more energy reserves and are therefore more resilient and more likely to survive than those in poorer condition (Clutton-Brock and Sheldon 2010; Cook et al. 2004). In females, reproductive traits such as litter mass, number of litters, neonatal mass, and breeding life-span increase with body condition (Atkinson and Ramsay 1995; Samson and Huot 1995). Therefore, evaluating body condition is of general biological interest but also has practical applications for the conservation and management of mammals.

The body condition of living mammals has been assessed with morphometric measurements (Cattet et al. 2002; Guinet et al. 1998), blood analyses (Gau and Case 1999; Hellgren et al. 1993), bioelectrical impedance (Farley and Robbins 1994; Hilderbrand et al. 1998), and ultrasound measurements of subcutaneous fat (Morfeld et al. 2014). However, these methods are unsuitable as a routine method because they require repeated capture of individuals. Applying these methods to free-ranging, large-bodied mammals is inherently difficult because the capture operation is dangerous for researchers and may affect animal behavior and survival through anesthesia and direct handling. An alternative, noninvasive evaluation method is body condition scoring (BCS). BCS is a subjective assessment of subcutaneous body fat stores based on a visual or tactile evaluation of muscle tone and key skeletal elements (Burkholder 2000; Otto et al. 1991). Various BCS systems have been established for monitoring individual condition in companion animals (*e.g.*, dogs and cats: Laflamme 2012), livestock (*e.g.*, cattle, horses, and pigs: Wildman et al. 1982; Henneke et al. 1983; Department for Environment Food and Rural Affairs 2004), and also wildlife (*e.g.*, bears, dolphins, and elephants: Joblon et al. 2015; Morfeld et al. 2014; Stirling et al. 2008). In addition, visual assessment criteria based on photographs have been used to evaluate relative body condition in whales. Photograph-based measurements of the length and width of gray whales (*Eschrichtius robustus*) from vertical aerial photogrammetry can reveal changes in body condition associated with fasting during winter migrations (Perryman and Lynn 2002). These studies demonstrate that it is possible to visually detect changes in body condition without capturing animals.

For killed or captured bears (*Ursus* spp.), a body condition index (BCI) has been established based on residuals from the regression of body mass against straight-line body length

(*i.e.*, the observed mass minus the expected mass: Cattet et al. 2002). Independently of sex or age, the BCI has a strong positive relationship with true body condition, defined as the combined mass of fat and skeletal muscle relative to body size (Atkinson et al. 1996; Cattet et al. 2002). The BCI has higher positive values for bears in better condition and lower negative values for those in poorer condition. In addition, predictive equations have been developed to estimate body mass and condition in bears from measurements of straight-line body length and axillary girth (Bartareau 2017; Moriwaki et al. 2018). However, to clarify seasonal and annual changes in the body condition of bears, it is necessary to develop a method that can be used to monitor body condition repeatedly and continued for several years. For proper conservation and management of bear populations, it is important to develop a noninvasive method of assessing body condition in bears without capture operations.

Here, this study developed a noninvasive method of evaluating the body condition of brown bears based on morphometric measurements obtained from photographs. The goal of this study was to develop an accurate, photograph-based evaluation method that could be applied to bears in various postures. To achieve this, the following three steps were taken. First, preliminary analyses were conducted using BCIs calculated from actual measurements of killed or captured bears to obtain fundamental information on the body condition of Hokkaido brown bears. It was also investigated whether the ratio of torso height to body length could be used as an indicator of body condition by examining its correlation with BCI. Second, the precision of photograph-based measurements was validated using photographs of an identifiable female. Four candidate methods of measurement were identified, including horizontal body length, Euclidean body length, polygonal-line body length, and horizontal torso length. Then, it was examined which method had the largest number of applicable photographs with sufficiently small variation in measurement. In addition, the ability of the photograph-based method to detect seasonal changes in body condition was examined. Third, the accuracy of the photograph-based measurement method was validated by examining the correlation between BCIs calculated from actual measurements of captured individuals and photographic evaluation of the same individuals.

MATERIALS & METHODS

Ethical approval

Field experiments were approved by Hokkaido Regional Environment Office and Kushiro Nature Conservation Office (Permit Number: 1606091 and 1705182). All bears were captured live in accordance with the Guidelines for Animal Care and Use of Hokkaido University

(Permit Number: 15009 and 17005) and all procedures were approved by the Animal Care and Use Committee of the Graduate School of Veterinary Medicine, Hokkaido University (Permit Number: 1152, 15009, and 17005). The protocols for capture received annual approval from the Ministry of the Environment, Japan, and the Hokkaido Government through research permit applications.

Study area

This study was conducted in the Shiretoko Peninsula, Hokkaido, Japan (Fig. 1-1). During 1998–2017, body masses and morphometrics were collected from brown bears captured for research purposes, killed for nuisance control, or harvested from the peninsula, including the towns of Shari and Rausu (Fig. 1-1). In addition, a focal survey was conducted in the Rusha area (Fig. 1-1), a special wildlife protection area. Body masses, morphometrics, and photographs of female bears were collected in the Rusha area during 2014–2018.

Bear capture and measurements

Bears were sampled each year during 1998–2017 between April and November. Most samples were obtained from bears killed for nuisance control or harvested, and some were obtained from bears captured for research purposes. The variables recorded for each bear included an identification code, date of measurement, location, body mass (kg), and straight-line body length (cm) (Supplemental Data S1). Body mass was measured with calibrated hanging spring scales. Body length was measured with a non-stretchable tape measure as the straight-line distance from the tip of the nose to the end of the last tail vertebra while the bear was aligned laterally. In addition, torso height (cm) was measured as the distance from the lowest point of the abdomen to the spine in females ≥ 5 years old during 2014–2017. Furthermore, tissue (*e.g.*, muscle and liver) from killed bears and blood and hair samples from captured bears were collected for DNA extraction, which allowed to identify individuals and their sex (Shimozuru et al. 2017; Shirane et al. 2018). Among 503 killed or captured individuals, 22 individuals were sampled more than once during the study period due to repeated capture or killing after capture; the following analyses used only the measurement taken at the greatest age.

The age in years of most bears captured or killed was estimated by counting the cementum annuli of the teeth (Yoneda 1976). For some individuals, the exact age could not be determined due to many cementum-layers developed in old individuals or poor quality of teeth samples. Individuals whose age range could only be estimated were excluded from the growth curve analyses but were included for BCI and subsequent analyses if the growth curve results (detailed below) allowed their classification into an age class. For example, females ≥ 5 years old were

excluded from growth curve analyses but were used as adults for subsequent analyses, whereas males ≥ 5 years old were excluded from all analyses.

Growth curve of body length

To estimate the age at which the growth of body length was completed, growth pattern in body length was examined using a von Bertalanffy curve as previously described in bears (Bartareau et al. 2011; Derocher and Stirling 1998; Derocher and Wiig 2002; Kingsley et al. 1988). The von Bertalanffy size-at-age equation was used in the form $A_t = A_\infty(1 - e^{-K(t-T)})$, where A_t is body length (in cm) at age t , A_∞ is asymptotic body length (in cm), K is a size growth rate constant (year^{-1}), and T is a fitting constant (extrapolated age at zero size; in years). F tests were conducted to determine whether the parameters of the von Bertalanffy growth equation differed significantly by sex. Analyses were conducted using FSA package version 0.8.30 (Ogle et al. 2020) and nlstools package version 1.0-2 (Baty et al. 2015) in R (R Core Team 2019). According to the age reaching 95% of the asymptotic body lengths obtained from this analysis (detailed below), bears were assigned to three age classes for each sex: cubs (0–1 years old), subadults (age 1–4 years and 1–7 years for females and males, respectively), and adults (age ≥ 5 years and ≥ 8 years for females and males, respectively).

BCI of killed or captured bears

BCI was calculated as previously described in Cattet et al. (2002). Specifically, body mass and length values were transformed to natural logarithms and a least-squares linear regression analysis was conducted to describe the relationship between the ln-transformed values. The standardized residuals of this linear regression were used as BCI. In addition, as a preliminary experiment for the evaluation of body condition using photographs, the ratio of torso height to body length (TH:BL) was calculated using actual measurement data.

Statistical methods. — To determine if the BCI was independent of body size, the correlation between BCI and body length, which is an indicator of body size (Cattet et al. 2002; Mahoney et al. 2001), was investigated. BCI was compared among seasons and age-sex classes using two-way analysis of variance (ANOVA). Tukey multiple comparisons (Tukey 1977) were used to evaluate differences between the mean values of each comparison. Based on major changes in diet (Ohdachi and Aoi 1987), the sampling period was divided into three seasons: spring (April to June; main diet of grass), summer (July and August; main diet of grass and ants), and autumn (September to November; main diet of berries and acorns). In addition, BCI was linearly regressed on the TH:BL of the same individuals, and the correlation coefficient was

calculated. Correlation analysis between TH:BL and body length was also used to investigate the effects of body size. All statistical analyses were conducted in R (R Core Team 2019).

Obtaining and filtering of photographs

Periodic surveys (≥ 1 day/2 weeks) have been conducted since 2011 in the Rusha area, mainly for monitoring the reproductive status of identifiable females (Shimozuru et al. 2017). In each survey, a field team of two to five people was formed, including at least one of the four core members with long experience with bears in the area. Field teams patrolled the area by car and waited for bears to emerge from the vegetation on the mountainside. When bears appeared, field teams followed individuals, maintaining a distance of about 20–100 m. Individual bears were identified by field staff according to their appearance as described in Shimozuru et al. (2017), and close-up photographs were taken from multiple angles with a digital, single-lens reflex camera (Nikon D800, NIKON Co., Tokyo, Japan; or Canon EOS 5D, Canon Inc., Tokyo, Japan).

For each survey in the Rusha area, lateral photographs of each individual bear were selected and graded based on several attributes: camera focus, camera tilt (vertical), camera angle (horizontal), body/torso height measurability, and body/torso length measurability for photography; and degree of body arch (vertical), straightness of body (horizontal), degree of neck flexing (vertical), and degree of neck bending (horizontal) for bear posture (Appendix 1-A, 1-B, and 1-D). Each photograph was given a score of 1 (good quality), 2 (medium quality), or 3 (poor quality) for each attribute. Photographs that were given a score of 3 for any attribute were removed from further analyses.

Morphometric measurements from photographs

ImageJ version 1.52a (Schneider et al. 2012) was used to extract morphometric measurements from lateral photographs of bears. The angle of the photographs was first adjusted according to the ground surface, then the torso height was measured in pixels (TH) as the distance perpendicular to the ground from the lowest point of the abdomen to the highest point of the waist (Fig. 1-2). Length measurements (in pixels) included the following four methods: the horizontal straight-line body length (HBL, Fig. 1-2) was the straight-line distance from the tip of the nose to the base of the tail; the Euclidean straight-line body length (EBL, Fig. 1-2) was the Euclidean distance from the base of the tail to tip of the nose; the polygonal-line body length (PBL, Fig. 1-2) was the sum of the distance from the base of the tail to the highest part of the shoulder parallel to the ground surface, from that point to the base of the ear, and from that point to the tip of the nose; and the horizontal straight-line torso length (HTL, Fig. 1-2) was the straight-line distance from the base of the tail to the highest part of the shoulder parallel to the ground. For all

measurements, any area that could be clearly judged to be only fur was excluded from the measurement range.

Precision of measurements from photographs

To examine the precision of each photograph-based measurement method and the effects of bear posture, photographs of one bear (bear ID: HC) that was monitored routinely in the Rusha area during 2016–2018 were used. Photographs were classified according to bear posture (Appendix 1-B and 1-D): photographs that had a score of 1 for all attributes were assigned to “Good”, those with a score of 2 for body straightness only were assigned to “BS”, those with a score of 2 for neck flexing only were assigned to “NF”, and those with a score of 2 for neck lateral bending only were assigned to “NB”. Photographs that were not assigned to any category were excluded from these analyses.

First, to determine the number of measurements sufficient to reduce measurement error, measurement precision within photographs was assessed by repeatedly measuring (50 times) the body morphometrics from the best photograph taken on September 25, 2017, and assigned to the “Good” category. From these measurements, the coefficients of variation (CVs) for TH, HBL, EBL, PBL, HTL, and the ratio of TH to body/torso length were calculated. In addition, by considering the standard deviation obtained from the 50 measurements as the population standard deviation, the measurement error was calculated at a given number of measurements. The minimum number of measurements was ultimately adopted, with a value of the measurement error that did not affect the second decimal place (*i.e.*, <0.0025). In the following analyses, TH and body/torso length were measured three times, and the TH:body/torso length ratio was calculated from the respective average values according to the results (detailed below).

Second, measurement precision between bear postures (differences between repeated measures of the same individual taken from photographs with different postures) was assessed by taking measurements from photographs in different posture categories. To eliminate the effects of seasonal changes in body condition, these analyses were restricted to photographs taken September 24–26, 2017. The TH:body/torso length ratio was compared among the posture categories for each measurement method with one-way ANOVA. Tukey multiple comparisons (Tukey 1977) were used to evaluate differences between the mean values of different categories. Then the CV of each method was calculated using all of the photographs applicable to the method to evaluate the measurement precision of each method. CVs among the four methods were compared using an asymptotic test (Feltz and Miller 1996). From these results, this study adopted the method that could be applied to photographs of the most diverse postures while maintaining a sufficiently high measurement precision between photographs (CV < 5%). In accordance with

these results (detailed below), TH:HTL was used as an indicator of body condition in the following analyses.

Third, to examine whether TH:HTL reflected seasonal changes in body condition, photographs taken between late June and early October during 2016–2018 were used. For each half-month, the best two or more photographs were selected and the median TH:HTL obtained from these photographs was considered the evaluation value for that half-month. TH:HTL among half-months was compared using one-way ANOVA and Tukey multiple comparisons (Tukey 1977) were used to evaluate differences between the mean values of each half-month. Statistical analyses were conducted using Microsoft Excel[®] (Microsoft Corporation 2016) or R (R Core Team 2019).

Accuracy of measurements from photographs

The accuracy of photograph-based measurement methods was examined using actual measurement data for seven females (≥ 5 years old) captured in the Rusha area (bear IDs: BE, DR, GI, KR, LI, RI, and WK). Photographs of these individuals were collected from within 3 days before and after the days the individuals were captured. After filtering the photographs, TH and HTL were measured and the TH:HTL ratio was calculated using two or more of the best photographs. BCI was also calculated using the body mass and length measured at the time of capture.

Statistical methods. —BCI was linearly regressed on the TH:HTL ratio and the correlation coefficient was calculated. Statistical analyses were conducted using Microsoft Excel[®] (Microsoft Corporation 2016).

RESULTS

This study weighed and measured 503 different individuals: 9 females from the Rusha area during 2014–2016 and 494 individuals (201 females and 293 males) from other parts of the Shiretoko Peninsula during 1998–2017. Among these, an age (in years) was assigned to 432 individuals (174 females and 258 males), and an age range was assigned to 56 individuals.

Body length growth curves

von Bertalanffy curves were successfully fitted to body length data for the 432 individuals with age (in years) assignments (Fig. 1-3, Table 1-1). The growth curves differed significantly by sex ($F_{3, 426} = 76.63, p < 0.001$). Females had achieved 95% of their asymptotic body length at 4.6 years of age, whereas males took 7.6 years to reach the same proportion. In accordance with these

results, 476 individuals, including those with known age ranges, were classified into age classes and used in the subsequent analyses: 8 females and 19 males were cubs, 105 females (1–4 years) and 211 males (1–7 years) were subadults, and 92 females ≥ 5 years old and 41 males ≥ 8 years old were adults.

BCI of killed or captured bears

Natural logarithmic transformation of the body mass and length data resulted in a linear relationship between mass and length as follows: $\ln \text{ body mass} = 3.04 \cdot \ln \text{ body length} - 10.40$ ($R^2 = 0.94$, residual standard deviation = 0.19, Fig. 1-4, Data S1). To facilitate estimation of BCI for brown bears, the following model was developed: $\text{BCI} = (\ln \text{ body mass} - 3.04 \ln \text{ body length} + 10.40)/0.19$. There was no correlation between body length and BCI ($r = 0.037$, $p = 0.39$), which indicates that BCI was independent of body size (Fig. 1-S2).

An ANOVA of BCI showed that BCI varied significantly by season ($F_{2,459} = 13.26$, $p < 0.001$; Table 1-2, Fig. 1-5), with bears sampled in spring and summer having lower BCI than bears sampled in autumn (both $p < 0.001$). Differences among age-sex classes were also significant ($F_{5,459} = 4.20$, $p < 0.001$): Adult males showed higher BCI than adult females ($p = 0.002$), subadult females ($p < 0.001$), and subadult males ($p = 0.003$), whereas BCI did not differ among other age-sex classes ($p = 0.35\text{--}0.99$). The interaction between season and age-sex class was not significant ($F_{9,459} = 0.46$, $p = 0.90$).

Measurements of torso height were obtained from 23 adult females. A positive correlation was found between the TH:BL ratio and BCI ($r = 0.81$, $p < 0.001$; Fig. 1-6). There was no correlation between body length and TH:BL ($r = -0.068$, $p = 0.73$), which indicates that TH:BL was independent of body size (Appendix 1-F).

Precision of measurements from photographs

A total of 220 photographs of the same bear (bear ID: HC) were taken September 24–26, 2017. After filtering based on photographic conditions and the body arch of the bear (Appendix 1-A, 1-B, and 1-D), 101 photographs remained. Of these photographs, 15 were assigned to “Good,” 9 to “BS,” 10 to “NF,” and 9 to “NB.”

Based on 50 repeat measurements of the best photograph in the “Good” category, the CV in measurement error within photographs was estimated to be 0.29% for torso height and 0.27%, 0.29%, 0.26%, and 0.45% for HBL, EBL, PBL, and HTL, respectively. For all measurement methods, the measurement error of the ratio of height to length was reduced to less than ± 0.0025 by measuring height and body/torso length ≥ 3 times (Table 1-3).

The torso height:body/torso length ratio differed among the posture categories for all measurement methods ($p < 0.001$ for TH:HBL and TH:EBL, $p = 0.005$ for TH:PBL, and $p = 0.002$ for TH:HTL, Table 1-4, Data S2). TH:HBL and TH:EBL obtained from photographs in the “BS,” “NF,” and “NB” categories differed significantly from the results obtained from photographs in the “Good” category (Table 1-4). TH:PBL measured using “BS” and “NB” photographs were different from those of “Good” photographs (Table 1-4). TH:HTL differed from “Good” photographs only when “BS” photographs were used (Table 1-4). When all photographs in each category that did not differ from “Good” for each method were used, the CV was $< 5\%$ for all methods and did not differ among methods ($p = 0.067$): 2.47% in TH:HBL (photo $n = 15$), 2.19% in TH:EBL ($n = 15$), 3.18% in TH:PBL ($n = 25$), and 3.93% in TH:HTL ($n = 34$). Given these results, TH:HTL was adopted as the measurement method with both the largest number of applicable photographs and a CV $< 5\%$ (*i.e.*, high measurement precision between photographs).

By calculating TH:HTL using photographs of the same bear (bear ID: HC) taken from late June to early October during 2016–2018, results determined that TH:HTL reached its lowest in late August (0.567 ± 0.012 ; mean \pm SE) and its highest in early October (0.714 ± 0.015 , Fig. 1-7). TH:HTL varied significantly among half-months ($F_{7,16} = 18.41$, $p < 0.001$) and was lower in early August than in late June ($p = 0.013$), early July ($p = 0.007$), late July ($p = 0.012$), early September ($p < 0.001$), late September ($p < 0.001$), or early October ($p < 0.001$).

Accuracy of measurements from photographs

Seven adult females were captured in the Rusha area during 2014–2016, and photographs of each individual were taken within 3 days before and after each capture date (Appendix 1-C). There was a positive correlation between BCI calculated from actual morphometric measurements and TH:HTL calculated from photographs ($r = 0.78$, $R^2 = 0.59$, $p = 0.041$; Fig. 1-8).

DISCUSSION

This study has developed a new method for visually assessing the body condition of adult female brown bears using photographs. The evaluation method consists of filtering photographs based on photograph conditions and bear posture and using photograph-based measurements of torso height and horizontal torso length in pixels to calculate the TH:HTL ratio. The strong positive relationship ($r = 0.78$, $R^2 = 0.59$) between TH:HTL calculated from photographs and BCI calculated from actual measurements of given individuals indicates that the body condition of brown bears can be estimated with a high degree of accuracy based on photographs. TH:HTL values increased as BCI increased, in agreement with other body condition indices, such as

Quetelet's index (Cattet 2000) and percent body fat (McLellan 2011). This study is the first to propose a photograph-based method of evaluating bear body condition that is accurate and reliable.

The most versatile photograph-based measurement method that could be applied to bears with various postures was the measurement not of body length but of torso length. In right whales (*Eubalaena* sp.) and gray whales, body condition has been evaluated with high precision and accuracy with aerial vehicle photogrammetry by selecting photographs under strict conditions based on the whale's posture (Christiansen et al. 2018; Perryman and Lynn 2002). However, it is not easy to collect a large number of good-quality photographs of brown bears inhabiting forests that are suitable for measurement. In fact, of the 220 photographs taken to confirm the precision of photograph-based measurement methods in this study, only 15 (6.8%) were classified into the "Good" category. Therefore, to establish a useful method of assessing body condition, it was necessary to find a method that had high applicability as well as high precision and accuracy. Although the body length of killed or captured brown bears is generally measured as the distance from the tip of the nose to the end of the last tail vertebra (Blanchard 1987), in the present study all methods that included the tip of the nose in the photograph-based measurement range (*i.e.*, HBL, EBL, and PBL) were affected by the degree of neck flexing and neck lateral bending. However, the torso length (*i.e.*, HTL) could be measured without being affected by the condition of the neck as long as the condition of body straightness was satisfied.

TH:HTL declined from June to August and increased thereafter until the end of the field survey in early October, which suggests that bears were gaining fat over this period. The period when TH:HTL was lowest (*i.e.*, August) coincides with the time when most cub disappearances occur in the Rusha area (Shimozuru et al. 2017), which indicates that poor nutrition in the summer may cause cub mortality. The seasonal changes in TH:HTL were partly consistent with BCIs calculated from killed bears, except that TH:HTL increased drastically in September. Because seasonal changes in TH:HTL were examined in only one individual in this study, it is necessary to examine how TH:HTL changes seasonally in other living bears. One factor leading to the difference between seasonal change patterns in TH:HTL and BCI may be differences in the food environment between the Rusha area and other areas. Acorns (*Quercus crispula*), which contain large quantities of carbohydrates and fats, are a major food source throughout Hokkaido during September–November (Ohdachi and Aoi 1987; Sato et al. 2005). In addition, the Rusha area is considered to be a natural "ecocenter", defined by Craighead et al. (1995) as an area where highly nutritional food is concentrated during a certain part of the year, and many bears are present in this area to obtain these resources, in particular salmonid fish, from late August (Shimozuru et al. 2017; Yamanaka and Aoi 1988). Therefore, bears in the Rusha area can consume higher-energy foods from late summer to autumn, which may cause their TH:HTL to increase more rapidly than

the BCI of bears killed in other areas. Another possible explanation for the difference in seasonal change patterns of body condition is that most of the actual measurements were collected from bears killed for nuisance control. Throughout the lower part of the peninsula, vast agricultural farms produce mainly dent corn and sugar beets. These farms may act as an attractive sink because of the availability of human-derived foods, which lead to human-caused bear deaths (Delibes et al. 2001; Sato et al. 2011). Therefore, there is a possibility that bears killed before September included those that had emerged into farmland or human residential areas to obtain anthropogenic foods to compensate for poor body condition. The results of this study suggest that including body condition data for living bears will improve estimations of seasonal and long-term trends in body condition and thus provide better estimates of the health of the bear population.

It is important to determine whether the method established using adult females in this study can be extended to other age-sex classes, other bear populations, and other bear species. Differences in body condition among age-sex classes should be taken into consideration. The results of this study showed that BCIs calculated from actual measurements were higher in adult males than in other age-sex classes. Therefore, relative changes in TH:HTL need to be examined by age-sex class. This study also showed no interaction between age-sex classes and seasons for BCI, which indicates that any age-sex class would show similar seasonal changes in body condition. However, it is necessary to investigate further whether the TH:HTL of other age-sex classes is able to show the seasonal changes that can be detected in adult females. Another consideration is differences in growth patterns between populations. Asymptotic body length (cm) was smaller in the Shiretoko Peninsula, 145.07 ± 1.48 and 179.47 ± 2.39 for females and males, respectively, than in two previously studied brown bear populations in northern Canada (171.55 ± 1.15 and 197.05 ± 0.69 , Bartareau et al. 2011) and Alaska (166.10 – 194.08 and 190.72 – 206.36 , Hilderbrand et al. 2018). Therefore, when using the photograph-based method to evaluate body condition in other populations, it is necessary to select target individuals depending on the age of maturity in each population.

Because the equipment needed to weigh large-bodied animals is often inadequate or unavailable in the field, it is more difficult to directly measure the body mass of brown bears than it is to take other morphometric measurements. The TH:BL ratio measured from killed or captured bears in this study was strongly correlated with BCI, which suggests that TH:BL, as well as axillary girth, which allows to estimate body mass (Bartareau 2017; Cattet 1990; Cattet and Obbard 2005; Derocher and Wiig 2002; Moriwaki et al. 2018), can be considered a useful indicator of body condition in captured bears without direct measurement of body mass. In mice, pelvic circumference is considered a potential predictor of fat content (Labocha et al. 2014). In addition, abdominal girth has been widely used in measurements of humans (*e.g.*, as part of

calculating body mass index). Although torso height is a nonstandard morphometric measurement in bear studies, such additional data may make it possible to improve predictions of body condition. Furthermore, using the photograph-based method, we can overcome the technical and financial difficulties of repeated capture and can conduct periodic assessments of body condition. A noninvasive evaluation method, BCS has been previously described for polar bears (*Ursus maritimus*; Stirling et al. 2008). However, BCS is a subjective assessment system and has the disadvantage of potentially missing small changes because it uses a scale from 1 to 5. Using morphometric measurements from photographs, the new method developed in this study makes it possible to conduct objective and quantitative visual assessments of body condition and allows researchers to identify small fluctuations in body condition.

This study was able to obtain usable photographs by conducting a survey in the Rusha area, where bears could be photographed easily and safely. An alternative way to apply this noninvasive photograph-based method to other populations in various locations is to collect photographs using an automated trail camera. A previous study has succeeded in measuring body dimensions from photographs of leopard (*Panthera pardus*) taken with an automated trail camera (Tarugara et al. 2019), while animal postures had a significant effect on measurement accuracy, as in the present study. To obtain a sufficient number of photographs with an animal posture that allows accurate measurements, future studies should consider recording videos rather than photographs with an automated trail camera. The challenge in applying the body condition assessment method to photographs or videos taken from automatic cameras is the selection of applicable individuals, *i.e.*, adult female brown bears. In previous studies investigating scent-marking patterns of brown bears with automated infrared cameras, age-sex classes were determined from images through the observation of the genitals, body size, body shape, and presence of young or drooping mammary glands (Clapham et al. 2014, 2012). In addition, by integrating automated trail camera surveys with noninvasive genetic sampling such as hair snagging, genetic analysis can be used to determine the sex of photographed individuals and to distinguish whether the individual has offspring (*i.e.*, whether the individual is sexually mature) (Sollmann et al. 2013). Furthermore, it has been reported that a deep learning approaches of facial recognition can be applied to identify individual brown bears (Clapham et al. 2020), indicating that individual selections and morphometric measurements from photographs can be more automated in the future.

CONCLUSIONS

This study developed a noninvasive method that uses photographs to assess the body condition of free-ranging brown bears and validated its accuracy against actual measurements of captured bears in the Shiretoko Peninsula, Hokkaido, Japan. Because this method is simple and applicable to photographs of bears in various postures, it can be widely applied and thus is useful for monitoring the body condition of brown bears repeatedly over the years. Using photograph-based evaluation will assist bear researchers in further investigating relationships among body condition, food habit, and reproductive success, which contribute to the conservation and management of brown bears.

Table 1-1. Parameter estimates (\pm SE) for von Bertalanffy size-at-age curves for the body lengths of 432 brown bears in the Shiretoko Peninsula, Hokkaido, Japan.

A_{∞} is the asymptotic body length, K is the size growth constant, and T is the theoretical age at which the animal would have size 0.

Sex	A_{∞} (cm)	K (year⁻¹)	T (years)	n
Female	145.07 \pm 1.48	0.51 \pm 0.04	-1.28 \pm 0.16	174
Male	179.47 \pm 2.39	0.32 \pm 0.02	-1.73 \pm 0.14	257

Table 1-2. Mean (\pm SE) body condition index (BCI) and body weight of brown bears in six age-sex classes captured and measured in the Shiretoko Peninsula, Hokkaido, Japan, during 1998–2017. Spring is April–June, summer is July and August, and autumn is September–November.

Season	Class	BCI	Weight (kg)	<i>n</i>
Spring	Female			
	Adult	-0.39 ± 0.26	98.5 ± 4.8	14
	Subadult	-0.39 ± 0.13	61.9 ± 5.4	27
	Cub	-	-	0
	Male			
	Adult	0.63 ± 0.35	230.1 ± 13.1	4
	Subadult	-0.15 ± 0.12	78.8 ± 4.0	77
	Cub	-0.30 ± 0.00	6.0 ± 0.0	1
	All classes pooled	-0.20 ± 0.00	81.7 ± 0.1	123
Summer	Female			
	Adult	-0.18 ± 0.12	101.4 ± 3.6	35
	Subadult	-0.20 ± 0.21	53.3 ± 4.1	46
	Cub	0.36 ± 0.48	10.8 ± 1.7	3
	Male			
	Adult	0.37 ± 0.14	213.4 ± 7.2	24
	Subadult	-0.01 ± 0.08	85.2 ± 5.5	91
	Cub	0.12 ± 0.45	11.5 ± 1.6	6
	All classes pooled	-0.03 ± 0.00	92.5 ± 0.1	205
Autumn	Female			
	Adult	0.20 ± 0.14	116.2 ± 4.1	43
	Subadult	0.17 ± 0.16	72.5 ± 6.2	32
	Cub	-0.08 ± 0.25	16.1 ± 0.7	5
	Male			
	Adult	1.16 ± 0.19	309.2 ± 13.2	13
	Subadult	0.51 ± 0.14	99.7 ± 6.6	43
	Cub	0.16 ± 0.33	22.4 ± 4.3	12
	All classes pooled	0.36 ± 0.00	107.9 ± 0.1	148

Table 1-3. Measurement precision within photographs of an adult female brown bear (bear-ID: HC) in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan. The standard error (SE) in the ratio of torso height to body/torso length at a certain number of measurements was calculated by considering the standard deviation (SD) obtained from 50 times measurements as the population standard deviation. CV means coefficient of variation.

Measurement	50 measurements		SE (number of measurement)		
	mean \pm SD	CV	(two)	(three)	(four)
TH:HBL	0.4316 \pm 0.0016	0.36%	0.0011	0.0009	0.0008
TH:EBL	0.4266 \pm 0.0015	0.35%	0.0010	0.0009	0.0007
TH:PBL	0.4163 \pm 0.0015	0.35%	0.0010	0.0009	0.0007
TH:HTL	0.7504 \pm 0.0040	0.53%	0.0028	0.0023	0.0020

TH, torso height; HBL, horizontal body length; EBL, Euclidean body length; PBL, polygonal line body length; HTL, horizontal torso length.

Table 1-4. Mean (\pm SD) ratio of torso height to body/torso length obtained from photographs of an adult female brown bear (bear-ID: HC) in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan. *P* values are based on comparisons of mean ratios from the “Good” category versus other categories for each measurement method with Tukey multiple comparisons. Bold characters indicate significant differences. The “Good” category contained photographs with a score of 1 for all attributes, “BS” had a score of 2 for body straightness only, “NF” had a score of 2 for neck flexing only, and “NB” had a score of 2 for neck lateral bending only.

Categories	<i>n</i>	mean \pm SD	CV	<i>p</i> -value
TH:HBL				
Good	15	0.416 \pm 0.010	2.47%	
BS	9	0.454 \pm 0.020	4.34%	<0.001
NF	10	0.444 \pm 0.015	3.38%	<0.001
NB	9	0.435 \pm 0.014	3.17%	0.028
TH:EBL				
Good	15	0.409 \pm 0.009	2.19%	
BS	9	0.431 \pm 0.017	4.00%	0.003
NF	10	0.428 \pm 0.014	3.18%	0.009
NB	9	0.428 \pm 0.014	3.25%	0.008
TH:PBL				
Good	15	0.394 \pm 0.011	2.88%	
BS	9	0.413 \pm 0.015	3.60%	0.010
NF	10	0.401 \pm 0.013	3.29%	0.586
NB	9	0.412 \pm 0.014	3.29%	0.023
TH:HTL				
Good	15	0.711 \pm 0.025	3.45%	
BS	9	0.762 \pm 0.034	4.46%	0.001
NF	10	0.721 \pm 0.028	3.86%	0.836
NB	9	0.736 \pm 0.028	3.74%	0.186

TH, torso height; HBL, horizontal body length; EBL, Euclidean body length; PBL, polygonal line body length; HTL, horizontal torso length.

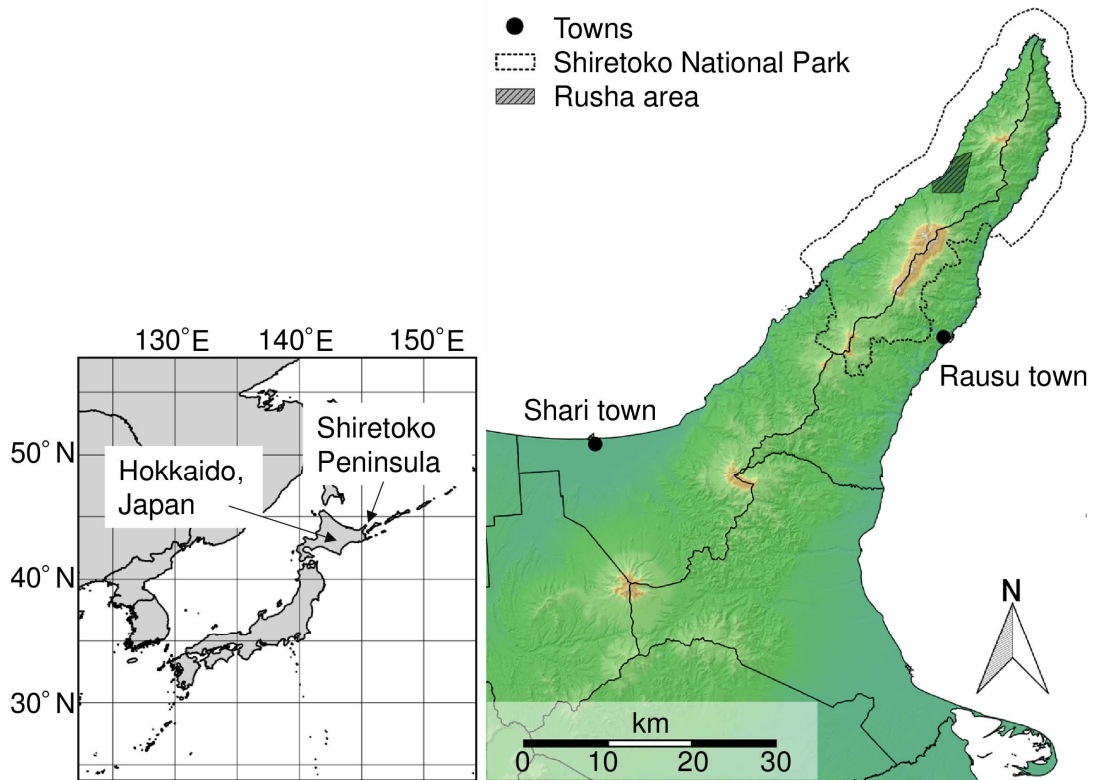
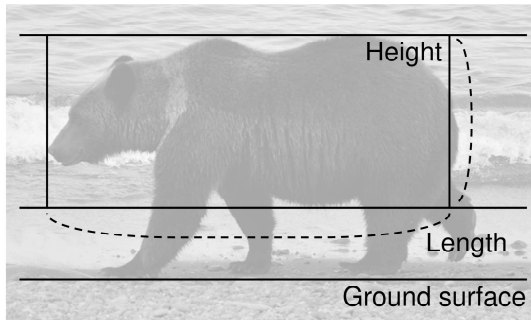
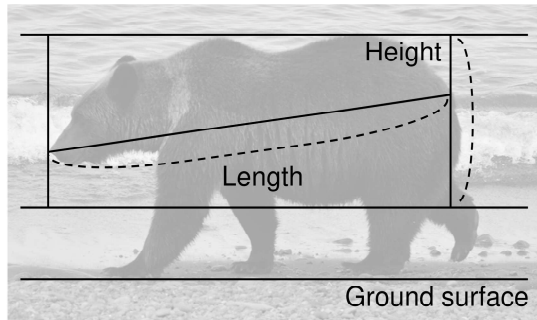


Figure 1-1. Map of the Shiretoko Peninsula, Hokkaido, Japan. The dotted line indicates the Shiretoko National Park. This map was created using QGIS version 2.16 (QGIS Development Team, 2017. QGIS Geographic Information System. Open-Source Geospatial Foundation Project. <http://qgis.osgeo.org>) and edited by the author. The base-map image, contour lines, topographic features are based on the National Land Numerical Information published by National Spatial Planning and Regional Policy Bureau, Ministry of Land, Infrastructure, Transport, and Tourism of Japan (available from <http://nlftp.mlit.go.jp/ksj/index.html>, accessed 7 December 2017).

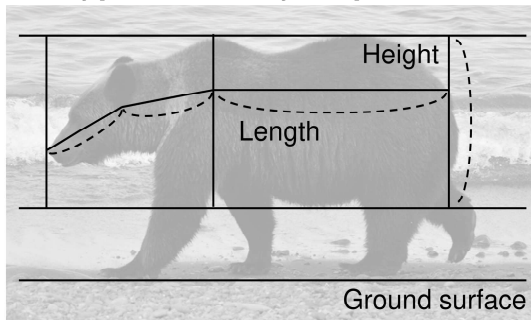
A. Horizontal Body Length (HBL)



B. Euclidean Body Length (EBL)



C. Polygonal-line Body Length (PBL)



D. Horizontal Torso Length (HTL)

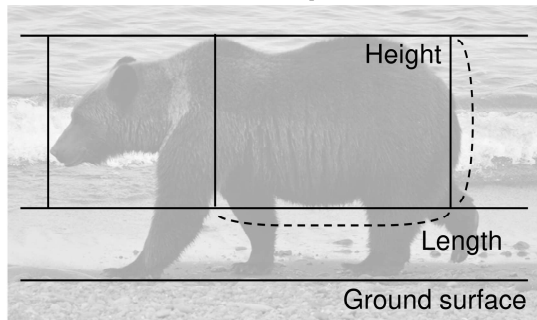


Figure 1-2. Four candidate methods of measurement to evaluate the body condition of brown bears in the Shiretoko Peninsula, Hokkaido, Japan. (A) Horizontal body length (HBL). (B) Euclidean body length (EBL). (C) Polygonal-line body length (PBL). (D) Horizontal torso length (HTL). Photo credit: Yuri Shirane.

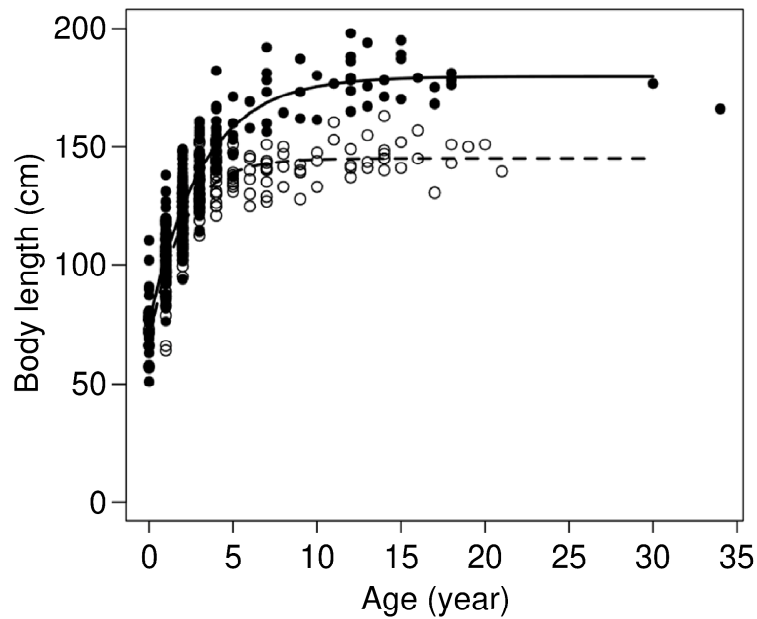


Figure 1-3. Body length at age for 174 female (○) and 258 male (●) brown bears in the Shiretoko Peninsula, Hokkaido, Japan. Fitted lines represent the von Bertalanffy growth curve for females (dashed line) and males (solid line).

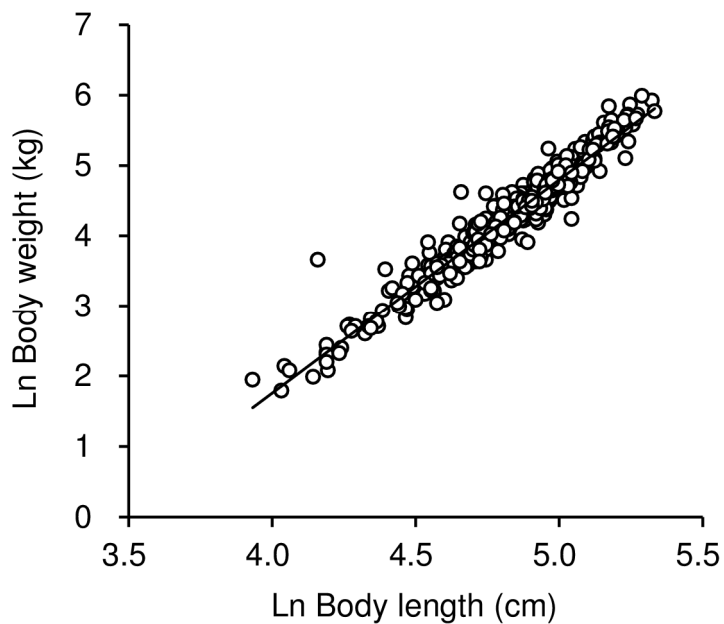


Figure 1-4. Relationship between ln-transformed body weight and ln-transformed body length for 476 brown bears killed or captured in the Shiretoko Peninsula, Hokkaido, Japan, during 1998–2017. The solid line indicates the best fitting line determined by ordinary least squares regression and is described as follows: $\ln \text{ body weight} = 3.04 \cdot \ln \text{ body length} - 10.41$ ($R^2 = 0.94$, residual standard deviation = 0.19).

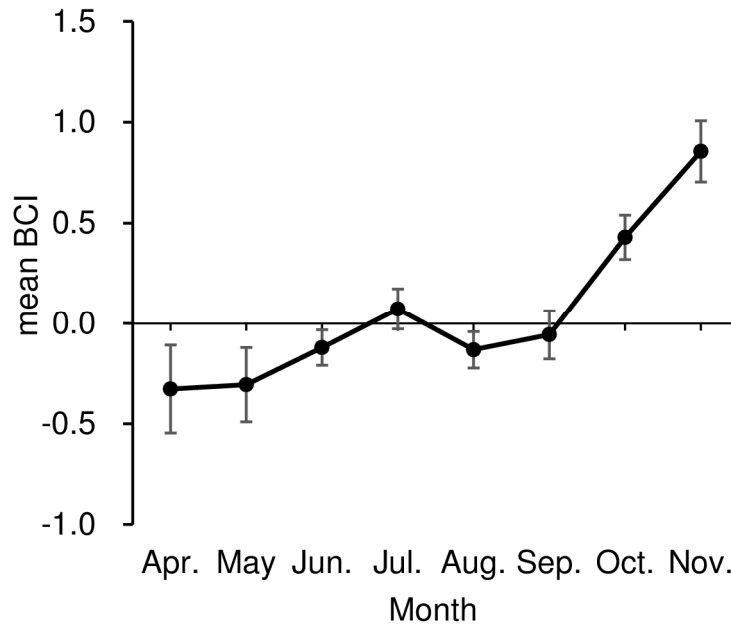


Figure 1-5. Monthly mean body condition index (BCI) of 476 brown bears killed or captured in the Shiretoko Peninsula, Hokkaido, Japan, during 1998–2017. Error bars show SEs.

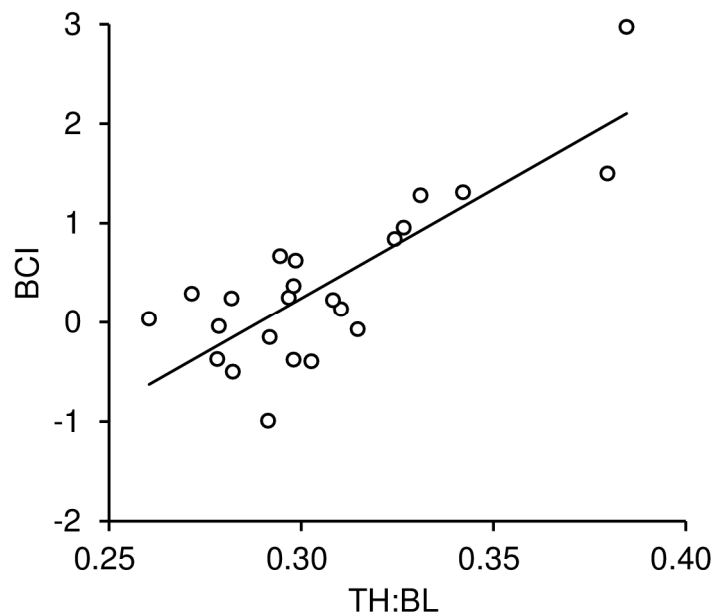


Figure 1-6. Relationship between torso height:body length ratio (TH:BL) and body condition index (BCI) for 23 adult female brown bears killed or captured in the Shiretoko Peninsula, Hokkaido, during 2014–2017. Pearson’s correlation was $r = 0.81$ ($R^2 = 0.65$, $p < 0.001$).

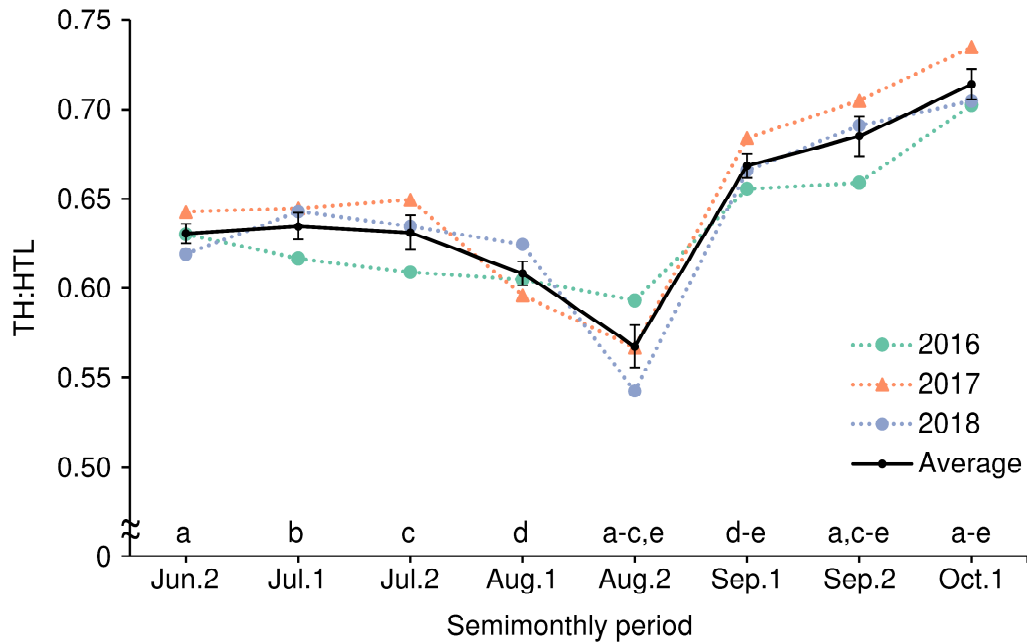


Figure 1-7. Seasonal changes in body condition estimated by calculating torso height:length ratio (TH:HTL) from photographs of an adult female brown bear in the Rusha area of the Shiretoko Peninsula, 2016–2018. TH:HTL was compared among half-months by one-way ANOVA with a post hoc Tukey multiple comparison test. Same letters indicate significant differences. Error bars show SEs.

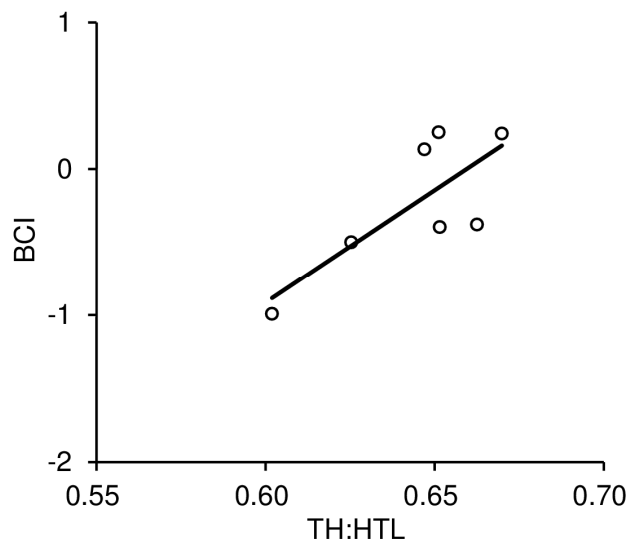


Figure 1-8. Relationship between torso height:length ratio (TH:HTL) and body condition index (BCI) for seven adult female brown bears captured in the Rusha area of the Shiretoko Peninsula, Hokkaido, 2014–2016. Pearson’s correlation was $r = 0.77$ ($R^2 = 0.59$, $p = 0.042$).

Appendix 1-A. Definition of photographing condition grades (scores) used for each photograph attribute to select photographs for assessing body condition. See Fig. 1-S1 for example pictures of each grade for each attribute of bear posture.

Attribute	Score 1 (good)	Score 2 (medium)	Score 3 (poor)
(A) Camera focus	The picture is sharp with the contour of the bear's body clearly visible.	The picture is blurry, but still clear enough to make out the contour of the bear's body.	The picture is too blurry to make out the contour of the bear's body.
(B) Camera tilt	The dorsal and ventral surface of the bear are vertical to the camera.	The dorsal and ventral surface of the bear deviate slightly from the vertical with the camera.	The dorsal and ventral surface of the bear deviates significantly from the vertical with the camera.
(C) Body angle	The body axis of the bear is perpendicular to the camera.	The body axis of the bear is angled slightly in the parallel plane, either back or forth.	The body axis of the bear is angled significantly in the parallel plane, either back or forth.
(D) Torso height measurability	Both the highest part of the waist and the lowest part of the abdomen are clearly visible.	The highest part of the waist or the lowest part of the abdomen is unclear or partly obscured, but can still be approximated.	The highest part of the waist and/or the lowest part of the abdomen are not visible due to another animal or object.
(E) Body/torso length measurability	The tip of nose (for HBL, EBL and PBL), the highest part of the shoulder (for PBL and HTL), and the base of tail are clearly visible.	The tip of nose, the highest part of the shoulder, or the base of tail is unclear or partly obscured, but can still be approximated.	The tip of nose, the highest part of the shoulder, and/or the base of tail are not visible due to another animal or object.

Appendix 1-B. Definition of bear posture grades (scores) used for each photograph attribute to select photographs for assessing body condition. See Fig. 1-S1 for example pictures of each grade for each attribute of bear posture.

Attribute	Score 1 (good)	Score 2 (medium)	Score 3 (poor)
(A) Body arch	No visible arching of the body. The bear stands parallel to the ground.	-	The legs or the central part of the body is significantly lifted or dropped.
(B) Body straightness	Right/left forelimb and hindlimb are in front of the other. The hip joint is not fully extended.	Right/left forelimb and hindlimb are inside the body or either of the legs is fully extended.	-
(C) Neck flexion	The angle between the ground surface and the line connecting the base of tail and the tip of nose is <13 degree.	The angle between the ground surface and the line connecting the base of tail and the tip of nose is ≥ 13 degree.	-
(D) Neck lateral bending	The neck of the bear is not bending laterally. The left and right ears are aligned.	The neck of the bear is bending to the side. The left and right ears do not overlap.	-

Appendix 1-C. The capture date and photographing period for seven adult female brown bears captured in the Rusha area of the Shiretoko Peninsula, Hokkaido, 2014–2016. Body condition index (BCI) was calculated from their actual measurements and the ratio of torso height to horizontal torso length (TH:HTL) was calculated from their photographs.

Bear-ID	Year	Capturing		Photographing		
		Date	BCI	Date	TH:HTL	<i>n</i>
BE	2015	4 July	-0.395	3–4 July	0.651	4
DR	2016	6 August	0.243	6 August	0.670	2
GI	2015	29 September	-0.992	29 September	0.602	4
KR	2014	25 August	0.252	25–28 August	0.651	2
LI	2016	5 July	-0.378	3–5 July	0.662	4
RI	2016	6 August	-0.499	6–7 August	0.625	4
WK	2016	4 July	0.135	1–4 July	0.647	4

(A) Body arch



(B) Body straightness



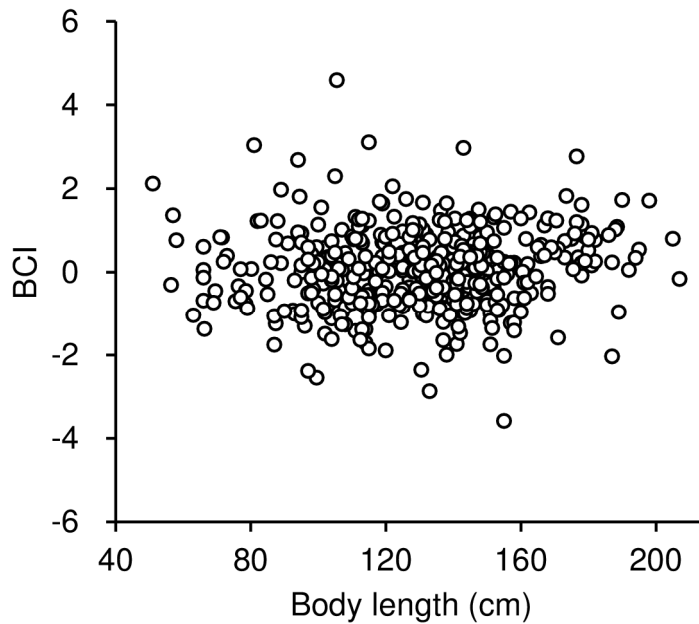
(C) Neck flexing



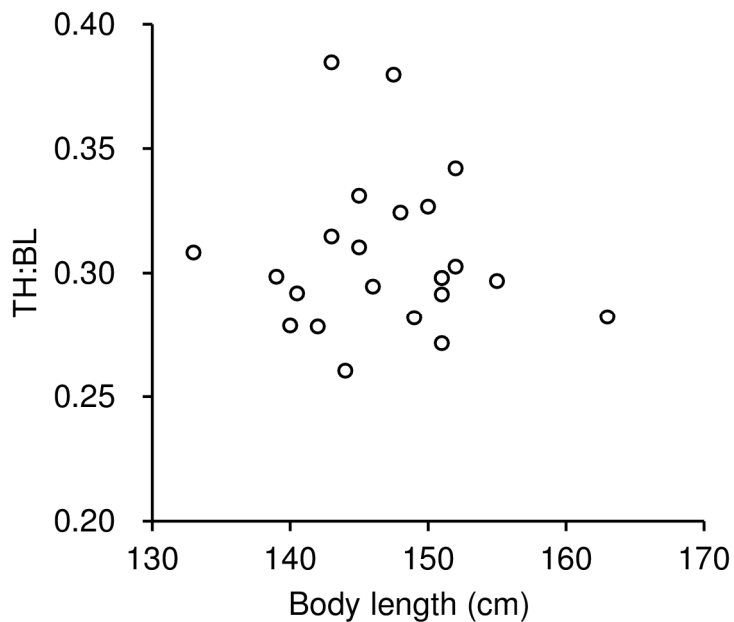
(D) Neck lateral bending



Appendix 1-D. Example photos for each photo score (grade) for the different photo attributes of bear posture used when filtering photographs for body condition analyses. (A) body arch, (B) body straightness, (C) neck flexing, and (D) neck lateral bending. See Appendix 1-B for definition of the different grades for each attribute. Photo credit: Yuri Shirane.



Appendix 1-E. Lack of association between the body condition index (BCI) and body length in 476 brown bears killed or captured in the Shiretoko Peninsula, Hokkaido, Japan, during 1998–2017. Pearson’s correlation values were $r = 0.037$ ($p = 0.39$).



Appendix 1-F. Lack of association between torso height:body length ratio (TH:BL) and body length in 23 adult female brown bears killed or captured in the Shiretoko Peninsula, Hokkaido, Japan, during 2014–2017. Pearson’s correlation values were $r = -0.068$ ($p = 0.73$).

SUMMARY

Body condition is an important determinant of health, and its evaluation has practical applications for the conservation and management of mammals. This study developed a noninvasive method that uses photographs to assess the body condition of free-ranging brown bears (*Ursus arctos*) in the Shiretoko Peninsula, Hokkaido, Japan. First, 476 bears captured during 1998–2017 were weighed and measured, and their body condition index (BCI) was calculated based on residuals from the regression of body mass against body length. BCI showed seasonal changes and was lower in spring and summer than in autumn. The torso height:body length ratio was strongly correlated with BCI, which suggests that it can be used as an indicator of body condition. Second, the precision of photograph-based measurements was examined using an identifiable bear in the Rusha area, a special wildlife protection area on the peninsula. A total of 220 lateral photographs of this bear were taken September 24–26, 2017, and classified according to bear posture. The torso height:body/torso length ratio was calculated with four measurement methods and compared among bear postures in the photographs. The results showed torso height:horizontal torso length (TH:HTL) to be the indicator that could be applied to photographs of the most diverse postures, and its coefficient of variation for measurements was <5%. In addition, when analyzing photographs of this bear taken from June to October during 2016–2018, TH:HTL was significantly higher in autumn than in spring/summer, which indicates that this ratio reflects seasonal changes in body condition in wild bears. Third, BCI was calculated from actual measurements of seven females captured in the Rusha area and TH:HTL from photographs of the same individuals. A significant positive relationship was found between TH:HTL and BCI, which suggests that the body condition of brown bears can be estimated with high accuracy based on photographs. This simple and accurate method is useful for monitoring bear body condition repeatedly over the years and contributes to further investigation of the relationships among body condition, food habits, and reproductive success.

CHAPTER 2

Dining from the coast to the summit:

Salmon and pine nuts determine

the summer body condition of female brown

bears on the Shiretoko Peninsula

INTRODUCTION

A variety of mammal species experience fluctuations in body condition as a result of varying energy intake and expenditure (Boswell et al. 1994; Fietz and Ganzhorn 1999; Parker et al. 2009). When highly nutritious food resources are available, individuals allocate excess energy to storage and increase or enhance their body condition. By contrast, severe nutritional restriction may lead to malnutrition with subsequent reduced survival and reproductive failure (Simard et al. 2008). Changes in energy intake and expenditure can be affected by seasonal and annual variation in food availability (Bojarska and Selva 2012), reproductive status (Rode et al. 2006), and climate change (Walther et al. 2002). Therefore, knowledge of the feeding ecology of an animal species and how its body condition changes as a result of environmental variation is critical to understand the ecology of the species and achieve effective management and conservation.

Some omnivore species consume a highly variable diet in response to spatial and temporal variation in food resources (Bojarska and Selva 2012; Mowat and Heard 2006; Vulla et al. 2009; Zalewska and Zalewski 2019). However, they often rely on seasonally restricted, highly nutritious foods such as soft mast, hard mast, and meat such as salmonid fish (Goszczyński et al. 2000; Hertel et al. 2018; Smith and Follmer 1972). The challenge is that mast production and upstream salmon abundance vary by year, and the resulting annual fluctuation in dietary content affects body condition, survival, and reproductive success as well as movement and habitat selection (Blanchard 1987; Helldin 1999; Noonan et al. 2014; Stenset et al. 2016; Welch et al. 1997; Zedrosser et al. 2006). For example, brown bears on the Kenai Peninsula depend on Pacific salmon (*Oncorhynchus* sp.) from June to October, and years when dietary salmon content is reduced correspond to years of decreased body fat content in adult females (Hilderbrand et al. 1999a). In addition, in the same population, females with dependent cubs or yearlings have a poorer body condition than lone females (Hilderbrand et al. 2000). Furthermore, in the Greater Yellowstone Ecosystem, whitebark pine (*Pinus albicaulis*) seeds account for the majority of the bear diet from about mid-August through the end of September, and annual variation in nut production has been linked to changes in bear movements (Blanchard and Knight 1991) and the number of incidents of bears damaging property and obtaining anthropogenic foods (Gunther et al. 2004). Because key foods and their effects on the body condition and behavior differ depending on the habitat and reproductive status of bears, the influence of dietary variability on body condition should be examined in various populations.

Although the Shiretoko Peninsula, Hokkaido, Japan (Fig. 2-1), contains high-quality brown bear habitat, human–bear conflicts, including agricultural crop depredation and intrusion into human residential areas, have become a serious problem. Over the past decade, an average

of 34 bears have been killed each year, mainly for management purposes (Kohira et al. 2009; Shimozuru et al. 2020). In 2012 and 2015, the number of bears killed for nuisance control was 65–67, nearly twice the usual number, and peaked in August (unpublished data). During the same summer, several thin bears and starved cubs were observed, indicating that poor nutrition due to a lack of summer foods might cause bears to intrude into residential areas in search of food. In addition, Shimozuru et al. (2017) revealed that most cub disappearances on this peninsula occur in July and August, which suggests that the main cause of cub mortality is deterioration of body condition in summer. Although Shiretoko brown bears have access to high-energy foods such as Japanese stone pine nuts in the subalpine zone and pink salmon spawning in the estuaries in summer (Ohdachi and Aoi 1987), it remains unknown how much these food resources from completely different environments contribute to energy intake each month. It is also unclear whether food habits vary by year and how such variation affects the body condition of bears. For proper conservation and management of brown bear populations, it is important to determine which food resources determine the body condition of bears and whether the effects of food shortages depend on the reproductive status of adult females.

The purpose of this study was to clarify seasonal and annual fluctuation in the body condition of adult female brown bears in relation to food habits and reproductive status. A 7-year longitudinal study that included scat sampling and direct observation of bears was conducted in a special wildlife protection area on the Shiretoko Peninsula. Using photographic evaluation to assess the body condition of free-ranging brown bears developed in Chapter 1 (Shirane et al. 2020), the body condition of identifiable bears was noninvasively monitored throughout the study period. This study tested the hypothesis that the body condition of adult female bears changes in response to shifts in food resources. Specifically, I predicted that body condition would reflect a cyclical annual pattern, declining through early to late summer, beginning to increase concomitantly with the onset of pine nuts or salmon consumption, and then peaking before hibernation. In addition, I predicted: (1) summer body condition would be the same every year; (2) it would be different every year; (3) it would be particularly poor in years when the consumption of both pine nuts and salmon was limited; and (4) it would be better in years when the consumption of both pine nuts and salmon was heavy. This study also explored the effects of reproductive status (*i.e.*, whether a female was alone or accompanied by offspring and the age of those offspring) on the seasonality of body condition. I predicted: (1) body condition would not differ depending on reproductive status; (2) females accompanied by cubs would exhibit the poorest body condition, followed by females with yearlings and then solitary females; (3) females accompanied by cubs or yearlings would exhibit a poorer body condition compared to solitary females; and (4) females accompanied by cubs would exhibit a poorer body condition compared

to solitary females and females with yearlings. Furthermore, I predicted that a poorer body condition in females with offspring would also mean that they would be more susceptible to food shortages compared to solitary females.

MATERIALS AND METHODS

Ethical approval

Field experiments were approved by Hokkaido Regional Environment Office and Kushiro Nature Conservation Office (Permit Number: 1606091 and 1705182). All procedures were conducted in accordance with the Guidelines for Animal Care and Use of Hokkaido University (Permit Number: 15009 and 17005) and were approved by the Animal Care and Use Committee of the Graduate School of Veterinary Medicine, Hokkaido University (Permit Number: 1152, 15009, and 17005).

Study area

Field research was performed in the Rusha area, near the tip of the Shiretoko Peninsula (Fig. 2-1), Hokkaido, Japan. This area is a narrow estuarine coast stretching south to north for approximately 3 km and has been designated as a special wildlife protection area where public access is prohibited without permission. Periodic surveys (≥ 1 day/2 weeks) were conducted in the Rusha area during 2012–2018.

Field methods

Field teams patrolled survey roads in the area (approximately 3 km, Fig. 2-1) by car and tracked bears when they appeared from the mountainside to observable places such as on the road or on the coast. Field teams kept a distance of about 20–100 m from them to avoid interruptions or effects on their natural behavior. Individual bears were identified by field staff according to their appearance (*e.g.*, size, color, facial characteristics, chest markings, and ear tags) as described in Shimozuru et al. (2017). This study focused on 12 adult female bears (≥ 5 years old; bear ID: BE, DC, DR, GI, HC, KB, KR, LI, RI, WD, WK, and WM) that could be easily identified and were frequently observed in the Rusha area throughout the surveillance period. When encountering these target bears, close-up photographs were taken from the lateral side using a digital single-lens reflex camera. In addition, three reproductive statuses of females were defined: females accompanied by cubs of the year, females accompanied by yearlings, and solitary females. When a cub disappeared from its mother, the cub was considered dead, as in other studies (Miller et al. 2003; Shimozuru et al. 2017; Swenson et al. 2001).

Fresh bear scats were collected when encountered in the Rusha area, mainly in low-altitude grasslands and coasts, and along survey roads leading to the area (approximately 9.5 km, Fig. 2-1) from June to November in each year during 2012–2018. The variables recorded for each scat included the collection date, location, and percent volume of each food item estimated visually (vFV). The time from defecation to scat collection (≤ 2 weeks) was estimated based on freshness in relation to recent weather conditions (*e.g.*, rain and sunshine) in order to classify the scats into one of five months from June to October. The field team in each survey included at least one of four core members who had extensive experience identifying the content of bear scat. In addition, scats encountered during 2013–2018 were collected individually in plastic bags and stored at -30°C for later analysis.

Laboratory analysis of diet

Scat samples were analyzed, except those in 2012 that were not collected, using the point-frame method (Sato et al. 2000). Each scat sample was filtered through a sieve (1.0 mm mesh) in running water. Materials remaining on the sieve were thoroughly mixed, and 30–90 g were evenly spread on a lab tray. The bottom of the tray consisted of a 1 cm grid, and the points of intersection were considered point frames. Each food item lying on points of intersection on the tray was identified, and the occupancy was calculated by dividing the number of points on which each item lay by the total number of points covered with all food items contained in the sample. For each sample, ≥ 200 points were counted, and the occupancy was used as the volumetric proportion in subsequent analyses. For scat samples containing salmon, however, we could not count ≥ 200 points for most samples because salmon had a high digestibility and most of the fecal content was washed away by washing. In consideration of this issue, we made the following exception only for scats containing salmon: even if the count number was < 200 points, the calculated occupancy was included in the following analysis when the wet weight of the scat sample was ≥ 50 g. Nonfood items were those deemed to have been ingested incidentally by bears (*e.g.*, anthill materials, twigs, wood fragments, needles from coniferous trees, and debris). Nonfood items also included bear hairs, with mean volumetric proportions per scat $\leq 0.5\%$ (Ciucci et al. 2014), which were presumably ingested during grooming. To eliminate interobserver bias, two trained observers performed the point-frame analysis.

Quantification of diet

The percent frequency of occurrence and the percent fecal volume were first determined for each food item semimonthly and monthly. Because not all food items are digested to the same extent, food items that are more difficult to digest might be overestimated, and easily digestible

food items might be underestimated (Hewitt and Robbins 1996). To prevent such bias, their contribution to the diet was also estimated in terms of ingested dry mass and energy content. The corresponding correction factors (CF_D , see Appendix 2-A for details; Hewitt and Robbins 1996; Dahle et al. 1998; Persson et al. 2001; Bojarska and Selva 2013; Stenset et al. 2016) were used to calculate estimated dietary content (EDC). To calculate estimated digestible energy content (EDEC), another group of correction factors (CF_E , see Appendix 2-A for details; Mealey 1980; Pritchard and Robbins 1990; Dahle et al. 1998; Persson et al. 2001; Ciucci et al. 2014; Stenset et al. 2016) were used. I did not calculate EDC or EDEC for nonfood items.

To investigate whether vFV estimated in 2012 could be compared to EDC estimated using the point-frame method in other years, data for scats collected in 2013–2018 were used to test the hypothesis that there would be no difference between vFV and EDC for any food category (*i.e.*, plants, drupes, berries, hard mast, pine nuts, mammals, salmon, and insects) in any month within the same year. I tested this hypothesis using a linear regression with no intercept and excluded the category from the annual comparison when the R^2 value was <0.70 . If the R^2 value was ≥ 0.70 , I conducted a t test ($p = 0.05$) between the slope of the regression equation and a theoretical slope of 1.0 for complete correspondence. If the null hypothesis that regression coefficient = 1 was not rejected, vFV was used as equivalent to EDC. If the null hypothesis was rejected, vFV was corrected based on the regression equations. According to the results (detailed below), the vFV obtained in 2012 was equated to EDC for all seven categories, except for mammals, and the “other” category was adjusted so that the corrected EDC for each month totaled 100%. Statistical analyses were conducted using R 4.0.2. (R Core Team 2020).

Estimation of body condition

Following Shirane et al. (2020), the body condition of adult female brown bears was assessed using morphometric measurements from photographs. Shirane et al. (2020) confirmed that this method accurately reflects the true body condition (*i.e.*, the body condition index obtained from the regression of body mass against body length) and has high measurement precision between photographs. However, this photograph-based method has the limitation that it is necessary to obtain photographs with sufficient photographic quality for morphometric measurements and with the posture of the bear that does not affect the evaluation value. To overcome this issue, lateral photographs of each individual bear were graded based on several attributes for photograph condition and bear posture (see Appendix 2-B for details; Shirane et al. 2020). Photographs were scored 1 (good quality), 2 (medium quality), or 3 (poor quality) for each attribute and those with a score of 3 for any attribute were removed from subsequent analyses. ImageJ version 1.52a (Schneider et al. 2012) was used to extract morphometric measurements

from lateral photographs of bears following protocols described in Shirane et al. (2020). Specifically, first the angle of all the photographs was adjusted according to the ground surface, then the torso height (TH) and the horizontal straight-line torso length (HTL) were measured in pixels: TH was the distance perpendicular to the ground from the lowest point of the abdomen to the highest point of the waist, and HTL was the straight-line distance from the base of the tail to the highest part of the shoulder parallel to the ground. TH and HTL were measured three times per photograph, and the ratio of TH to HTL (TH:HTL) was calculated from the respective average values. For each of eight sessions (June, July, early August, late August, early September, late September, October, and November), TH:HTL was calculated using at least two photographs per individual, and the median of these was used as an indicator of body condition. We included bear-years with TH: HTL data for at least 2 out of 8 sessions per year in the analysis. Bear-years for which TH:HTL data were available for only one session in a particular year were excluded from the analyses. In addition, if the reproductive status would affect the body condition of female bears, their body condition may differ before and after the loss of the offspring. To eliminate this effect, when females had lost their dependent young by either death or family break-up, any data for subsequent sessions of these females were excluded from the following analyses.

Statistical analyses

I distinguished between years in which pine nuts and salmon constituted major dietary content and years in which they did not. First the period of major consumption of pine nuts and salmon was estimated based on the mean EDC of pine nuts and salmon for each month during 2013–2018. Using a threshold EDC value of 20% (Ciucci et al. 2014; Mattson et al. 2004), the month in which the mean EDC exceeded the threshold was considered as the major consumption period. Then years were classified as either high or low consumption of pine nuts and salmon depending on whether those EDC values in the major consumption period during 2012–2018 exceeded the mean EDC.

Differences in body condition among sessions were examined with generalized linear mixed-effects models, as these models are flexible enough to account for different numbers of observations per individual. I used TH:HTL as the response variable and included year and bear ID as random effects on the intercept and month as a fixed effect. I used analysis of variance with Satterthwaite's method and Bonferroni multiple comparisons.

Generalized additive mixed models (GAMM, smoothing analyses; Zuur et al. 2009) were used to identify nonlinear effects of session on body condition and the relationships among body condition, dietary content, and reproductive status. In each GAMM, the response variable (TH:HTL) was run with the Gaussian family and identity link, and bear ID was included as a

random effects smooth term to account for correlation due to repeated measures. Because there are previously reported effects of month of year on bear body condition in the Rusha area (Shirane et al. 2020), a null model without session would not make biological sense. Hence, session (starting from June: 1, 2, 3, 3.5, 4, 4.5, 5, and 6) was included in all models. Thin-plate regression splines were used to fit session, in which the beginning and end points of a cycle were not constrained by each other (Zuur et al. 2009). Model selection involved comparing Akaike's information criterion corrected for small sample size (AIC_c) values between a set of ecologically relevant candidate models defined *a priori* (Burnham and Anderson 2002).

The model selection was divided into three stages. First, I assessed whether body condition varied by dietary content (Stage 1). I set models based on four predictions and selected a best-fit model (that with smallest AIC_c value). Second, I tested whether body condition varied by reproductive status based on four predictions (Stage 2). Third, The combined effects of diet and reproductive status (Stage 3) were assessed using factors in the best-fit models from Stages 1 and 2. All statistical analyses were performed in R with the lme4 (Bates et al. 2015), emmeans (Lenth 2020), and mgcv (Wood 2011) packages. The statistical models were validated by plotting model residuals versus the fitted values (Zuur et al. 2009).

RESULTS

Scat collection and analysis

A total of 2,079 scats (267, 403, 552, 507, and 350 for each month from June to October, respectively) were collected, including 315 analyzed visually in 2012 and 1,764 analyzed using the point-frame estimation during 2013–2018. vFV was positively correlated with EDC calculated using the point-frame method (Appendix 2-C). The R^2 values obtained by regression analysis were more than 0.80 for all food items with the exception of mammals ($R^2 = 0.12$, Appendix 2-C). The slope of the regression equation differed significantly from the theoretical slope of 1.0 for plants ($t_{28} = 2.61$, $p = 0.015$), drupes ($t_{28} = 2.65$, $p = 0.013$), berries ($t_{28} = 4.80$, $p < 0.001$), and pine nuts ($t_{28} = 4.31$, $p < 0.001$) but did not differ for hard mast ($t_{28} = 0.60$, $p = 0.554$), salmon ($t_{28} = 1.63$, $p = 0.114$), and insects ($t_{28} = 0.44$, $p = 0.664$). Therefore, the vFV for hard mast, salmon, and insects was used as equivalent to EDC in the following analyses. In addition, vFV was corrected based on the regression equations for plants, drupes, berries, and pine nuts and used these values as equivalent to EDC in the following analyses. I excluded 2012 data from the summary of monthly diet composition (Table 2-1 and Fig. 2-2), as vFV could not be approximated to EDC in the mammal category.

Seasonal and annual variation in diet

A trend was observed of monthly changes in bear diet (Table 2-1 and Fig. 2-2). Plants consistently dominated the diet in June and July, with peak consumption in June. Insects (primarily ants) contributed an average of 36.4% EDEC in July, when their monthly consumption was highest. Mammals (primarily sika deer, *Cervus nippon yesoensis*) were also used, with peak consumption in June, although their contribution to EDEC was only 12.0%. Consumption of overwintering hard mast in June and July was generally low. In August, although bears continued to consume plants and insects, nuts of Japanese stone pine dominated the diet, providing an average of 39.8% EDEC. In addition, salmon began to be consumed by bears in August, accounting for the fourth largest contribution to EDEC (14.4%). Salmon consumption was highest in September and contributed an average of 46.1% EDEC. Hard mast and berries were also consumed from September, with peak consumption in October. The hard mast category comprised almost exclusively *Q. crispila* acorns, whereas the berries category included various species such as wild vine (*Vitis coignetiae*) and hardy kiwi (*Actinidia* spp.). On average, the major consumption periods for pine nuts and salmon were August and September, respectively.

Annual differences in bear diet were observed in August and September (Fig. 2-3). Based on the EDC of pine nuts in August, 2013 (47.4%), 2014 (47.5%), 2016 (47.3%), and 2018 (42.9%) were identified as years with above-average consumption (34.9%), and thus I considered them heavy-consumption years. Similarly, 2013 (54.4%), 2016 (65.4%), and 2018 (72.2%) were identified as years with large consumption of salmon; all of these years also involved heavy consumption of pine nuts.

Factors affecting body condition

A total of 1,226 photographs of 12 adult females were analyzed during 2012–2018. On average, 3.6 photographs of each individual were used per session. When data for all years during 2012–2018 were pooled, at least 9 of the 12 females were evaluated for body condition in each session. TH:HTL differed significantly among sessions ($p < 0.001$, Fig. 2-4). It exhibited a general decline in June and August, followed by an increase from September to November (Fig. 2-4, Appendix 2-D).

TH:HTL showed different seasonal patterns in years with high consumption of both pine nuts and salmon (Table 2-2 and 2-3; Stage 1). In addition, TH:HTL differed depending on whether females were accompanied by dependent young (Table 2-2 and 2-3; Stage 2), and body condition was poorer for females with offspring than for solitary females. The model improved slightly when both diet and reproductive status were included (Table 2-3; Stage 3). The final best-fit model revealed that bears experienced smaller seasonal fluctuations in TH:HTL when they exhibited

heavy consumption of both pine nuts and salmon compared to when salmon consumption was low ($edf = 3.89$ and 5.61 , respectively; Table 2-4). When the consumption of both pine nuts and salmon was heavy, TH:HTL declined very little, reaching the lowest point in early August and peaking in November (Fig. 2-5). However, TH:HTL continued to decline until late August when salmon consumption was light. Furthermore, it was lower for females with offspring than for solitary females ($\beta = 0.020$, standard error = 0.004 , $t = 5.16$, $p < 0.001$, Table 2-4).

DISCUSSION

This report is the first to quantify in detail the food habits of brown bears from early summer to early autumn on the Shiretoko Peninsula. Shiretoko bears mainly use herbaceous plants in early summer and berries and hard mast in autumn, which is similar to patterns reported in brown bear populations around the world (Mattson et al. 1991; McLellan and Hovey 1995; Stenset et al. 2016). However, in late summer, when the nutritional value of herbaceous plants decreases (Cicnjak et al. 1987) and berries are still immature, bears eat a variety of foods depending on their population, including premature herbaceous plants in cooler areas (Munro et al. 2006; Rodríguez et al. 2007) and alternative foods such as anthropogenic foods (Piédallu et al. 2016; Sato et al. 2005). This study found that pine nuts and salmon contributed a high percentage to the diet of brown bears on the Shiretoko Peninsula in August and September, respectively. This is not consistent with the food habits of bears in other Hokkaido populations that rely on herbaceous plants, berries, or crops in late summer (Aoi 1985; Matsubayashi et al. 2014; Ohdachi and Aoi 1987; Sato et al. 2005, 2004; Sato and Endo 2006). Although consumption of pine nuts was also reported in a brown bear population on Mt. Daisetsu (with a summit reaching an altitude of 2,000 m; Ohdachi and Aoi 1987), current study demonstrates that brown bears on the Shiretoko Peninsula are unique in that they consume both pine nuts and salmon. Yellowstone National Park (with an altitude of 1,600 to 3,300 m) is also an area where bears eat both whitebark pine nuts in subalpine forests from about mid-August through the end of September and cutthroat trout (*O. clarki*) in streams entering Yellowstone Lake from June to July (Mattson et al. 1991). However, the observations on the Shiretoko Peninsula in this study are unique in that consumption of pine nuts and salmon by bears was concentrated in August and September. In addition, considering that altitudes of about 100 m are the upper limit of salmon run-up in Hokkaido (Urabe et al. 2013), these results have demonstrated that the Shiretoko Peninsula is the only region in the world where brown bears depend on food in extremely different environments such as coasts and the subalpine zone in late summer. Scat samples collected in the Rurua area along the coastline contained a large amount of pine nuts, which suggests that brown bears frequently travel between coastal

areas and subalpine zones in late summer and do not solely feed on pine nuts during random encounters.

The combination of scat analysis and photographic evaluation of body condition used in this study proved useful for noninvasive long-term monitoring of free-ranging brown bears. Scat samples permit identification of the species of food item and quantification of the dietary content of bears. This made it possible to focus on specific food items, pine nuts and salmon, and compare their consumption by season and year. This study estimated the detailed food habits of bears at the population level in a limited area by intensively sampling the Rusha area. On the Shiretoko Peninsula, a male-biased dispersal pattern of brown bears has been previously reported, and females are philopatric (Shirane et al. 2019, 2018). In addition, a genetic survey was previously conducted throughout the peninsula (Shirane et al. 2018), and the 12 adult females used for photographic evaluation in this study were not detected in other areas, except for one individual (bear ID: WM) that was killed for nuisance control on the east side of the peninsula. Based on this information, the content of scat collected in the Rusha area is considered to reflect the typical food habits of the 12 female brown bears targeted in this study.

This study provides insight into seasonal patterns in body condition in brown bears in relation to food condition dynamics. I found evidence that body condition continued to decline into late August and then increased to a peak before denning, which indicates that fluctuations were related to seasonal resource availability. Spring is considered a negative foraging period because bears face the costs of maintenance, growth, and cub rearing in the spring (Hilderbrand et al. 2000) and many wild bears lose fat and lean tissue during this time period (Blanchard 1987; Eagle and Pelton 1983; Hellgren et al. 1989). Similar to previous studies, the findings from this study suggest that available spring to early summer food resources (*i.e.*, plants and insects) provide insufficient energy for Shiretoko brown bears to maintain their body condition after den emergence. In September, when salmon consumption increased, body condition started to increase as predicted. Around the same time, brown bears were consuming a variety of high-energy foods, such as soft and hard mast, and rapidly depositing fat. Although salmon consumption decreased and acorns dominated the diet in October, body condition continued to improve until November, which indicates that overconsumption of a high-energy but low-protein diet contributes extra energy to fat deposition, as suggested by Felicetti et al. (2003).

The body condition of the bears began to recover later on the Shiretoko Peninsula (*i.e.*, in September) compared to bear populations in British Columbia (in August; McLellan 2011) and Yellowstone National Park (in July; Schwartz et al. 2014). Hokkaido brown bears emerge from their dens between March and May, which is similar to the timing of den emergence in British Columbia (in April–May; Ciarniello et al. 2005) and Yellowstone (in late March; Judd et al. 1986).

Therefore, the period of poor body condition is longer in Hokkaido brown bears than in other populations. This difference may depend on when high-energy foods become available in summer. Fruits account for more than 70% of the bear diet from early July to September in British Columbia (McLellan and Hovey 1995). In Yellowstone, whitebark pine nuts dominate the diet from mid-August through the end of September, and bears consume cutthroat trout in June and July, although in small amounts (Mattson et al. 1991). In contrast, Shiretoko bears did not consume pine nuts until August, with an EDC of only 34.9%. Although the Shiretoko Peninsula harbors diverse and abundant food resources for brown bears, the availability of high-quality foods occurs primarily during autumn; therefore, they likely experience a particularly harsh summer compared to brown bears in other locations.

Annual differences in dietary content created different seasonal patterns of body condition. The seasonal patterns of body condition differed between the years when both pine nut and salmon consumption were high and the years when they were not. In the years with high consumption of both food items, body condition began to recover earlier, resulting in a better summer body condition. Even in years with heavy pine nut consumption and low salmon consumption (2014), body condition exhibited the same seasonal pattern as in years when the consumption of both was low (2012, 2015, 2017). Because data set obtained in this study during 2012–2018 did not contain years when consumption of pine nuts was low and salmon consumption was high, I cannot determine whether the difference in body condition seasonality was caused by salmon alone or both salmon and pine nuts. However, considering that body condition began to recover in August in years with good food conditions, it is reasonable to assume that pine nuts in August also contribute to the recovery of body condition. I can expect that body condition in late August will not be good, even if only salmon is consumed heavily. Eating a large amount of both pine nuts and salmon enables rapid recovery, despite the aforementioned harsh summers of the Shiretoko Peninsula.

Female bears with dependent offspring exhibited a poorer body condition than solitary females. I propose two potential reasons for this. First, pregnant bears must invest in their cubs to give birth and subsequently to lactate (*i.e.*, high energy expenditure). Females with cubs of the year have a lower lean body mass than solitary females in the spring (Hilderbrand et al. 2000), with increased costs of protein catabolism due to lactation demands (Wright et al. 1999). Second, females with cubs of the year can move only limited distances in search of food resources (*i.e.*, low energy intake). The movement rate of adult female brown bears in Sweden is slower when they are accompanied by cubs than when they are solitary (Martin et al. 2013; Steyaert et al. 2014). Although the results of this study suggest that brown bears frequently travel between the subalpine region and the coastline for foraging, further research is needed to clarify whether such movement

is even possible for females with cubs and whether habitat selectivity differs depending on reproductive status.

The results of this study demonstrate that both dietary content and reproductive status are the primary determinants of seasonal and annual variation in the body condition of brown bears. The final best-fit model indicated that females with offspring exhibit particularly poor condition in late August in years with light consumption of pine nuts or salmon. This finding has important implications not only for seasonal and annual fluctuation in body condition but also for the long-term survival of the Shiretoko brown bear population. In the Rusha area, the worst season for body condition (August) coincided with the period with the highest mortality rates for cubs of the year (Shimozuru et al. 2017). This finding is consistent with the claim that cub mortality is mainly due to poor nutrition in summer rather than infanticide by adult males in the Rusha area. In Hokkaido, many factors that imply effects of climate change on ecosystems have been observed, such as decreased seasonal sea ice (Makino and Sakurai 2012), reduction in the body size and population of salmon (Kaeriyama 2008; Kishi et al. 2010), and decreases in habitats of stone pine (Horikawa et al. 2009). In Yellowstone National Park, mountain pine beetle (*Dendroctonus ponderosae*) outbreaks promoted by warmer temperatures have caused mortality within about 82% of the whitebark pine stands (Macfarlane et al. 2013), resulting in a reduction of the digestible energy and protein content of the brown bear diet (López-Alfaro et al. 2015). Additionally, less sea ice due to global warming reduces the seal hunting opportunities for polar bears, resulting in lighter body mass of female polar bears and fewer offspring (Amstrup et al. 1986; Derocher et al. 2011; Stirling et al. 1976; Stirling and Derocher 1993). It is necessary to continue to monitor long-term trends in the food environment and body condition of brown bears to better understand population dynamics on the Shiretoko Peninsula.

CONCLUSIONS

This study has revealed that subalpine pine nuts and coastal salmon, which are foods unique to the Shiretoko Peninsula, determine the summer body condition of female brown bears. In addition, August is the harshest season for brown bears on the peninsula, in particular when bears cannot heavily consume salmon. These findings may help to clarify the cause of human–bear conflict in Shiretoko, but it is still debatable whether food shortages and poor nutrition trigger the intrusion of bears into human residential areas. A previous study revealed that American black bears (*Ursus americanus*) use areas of higher human density in years when mast food production is poor in Colorado, USA (Baruch-Mordo et al. 2014). By contrast, another study suggested that mast production does not determine brown bear movement behavior in Sweden (Hertel et al.

2019). The relationships among diet, body condition, and the behavioral patterns of bears need to be investigated further to establish effective management strategies for the mitigation of human–bear conflicts. In addition, females with offspring are particularly vulnerable to the adverse effects of food shortages in summer, which implies that significant declines in summer food resources may directly reduce foraging opportunities and negatively affect reproductive success. These findings have important implications for predicting changes in reproductive success and behavioral patterns of brown bears with respect to annual fluctuation and even long-term declines in the availability of coastal and subalpine foods.

FLUCTIATION IN DIET AND BODY CONDITION

Table 2-1. The mean seasonal diet of brown bears in the Rusha area based on analyses of 1,764 fecal samples collected during 2013–2018. Data are estimated dietary content (EDC) and estimated dietary energy content (EDEC). Contributions <0.05% are indicated by “tr” (trace) for clarity.

Food item ^a	June (n = 242)		July (n = 308)		August (n = 476)		September (n = 466)		October (n = 272)	
	EDC	EDEC	EDC	EDEC	EDC	EDEC	EDC	EDEC	EDC	EDEC
Plants	76.4	60.8	47.7	33.1	24.7	14.8	5.3	2.6	2.4	1.1
Herbaceous plants	70.4	56.0	46.4	32.1	24.2	14.6	5.2	2.6	2.3	1.1
Woody plants	5.9	4.8	1.3	0.9	0.5	0.3	tr	tr	0.1	tr
Seaweed	tr	tr	0.1	tr	tr	tr	-	-	-	-
Pine nuts										
<i>Pinus pumila</i>	-	-	2.8	4.2	34.9	39.8	7.0	7.2	-	-
Drupes	tr	tr	6.9	5.2	6.6	5.2	8.2	6.4	0.3	0.2
<i>Prunus sargentii</i>	-	-	5.9	4.3	0.4	0.2	-	-	-	-
<i>Prunus ssiori</i>	-	-	1.0	0.8	4.4	3.0	4.5	2.7	0.2	0.1
Berries	0.3	0.6	2.4	3.2	4.2	5.2	15.2	16.3	31.8	32.4
<i>Vaccinium</i> spp.	-	-	0.1	0.1	tr	tr	-	-	-	-
<i>Morus australis</i>	-	-	0.5	0.7	0.1	0.1	-	-	-	-
<i>Vitis coignetiae</i>	-	-	tr	tr	2.1	2.6	7.8	8.4	5.7	5.8
<i>Sorbus commixta</i>	-	-	-	-	1.0	1.1	3.3	3.5	4.4	4.5
<i>Actinidia</i> spp.	-	-	-	-	0.5	0.7	2.7	2.9	17.1	17.4
<i>Aralia</i> spp.	-	-	-	-	tr	tr	0.9	1.0	-	-
<i>Phellodendron</i> <i>amurense</i>	-	-	-	-	-	tr	0.3	0.3	3.3	3.4
Hard mast and nuts	6.7	10.3	5.2	6.3	0.9	1.0	19.6	20.8	47.4	47.8
<i>Quercus crispula</i>	6.6	10.1	5.2	6.3	0.8	0.9	14.1	14.9	45.1	45.5
<i>Juglans mandshurica</i>	0.1	0.1	-	-	0.1	0.1	5.4	5.8	2.2	2.2
Insects	6.3	10.5	24.6	36.4	12.1	14.8	0.3	0.4	0.4	0.5
Formicidae	5.3	9.0	23.0	34.0	11.3	13.9	0.1	0.1	-	-
Vespidae	0.2	0.3	0.1	0.1	0.4	0.5	0.2	0.2	0.1	0.1
Diptera	0.7	1.1	0.8	1.3	0.1	0.1	tr	tr	-	-
Mammals	6.9	12.0	3.0	4.5	0.5	0.6	0.2	0.2	1.0	1.1
<i>Cervus nippon</i> <i>yesoensis</i>	6.1	10.7	2.0	2.9	0.3	0.4	0.1	0.1	0.8	0.8
<i>Ursus arctos</i> ^b	tr	0.1	0.5	0.8	0.2	0.1	-	tr	tr	tr
Salmon										
<i>Oncorhynchus</i> spp.	-	-	0.1	0.1	12.2	14.4	44.2	46.1	16.7	17.0
Other	3.4	5.8	7.2	7.0	4.0	4.1	0.1	0.1	tr	tr
Fungi	0.1	0.1	3.3	1.3	0.8	tr	-	-	-	-
Birds	0.9	1.5	0.2	0.3	0.6	0.8	-	tr	-	-
Shellfish	0.9	1.5	1.6	2.3	1.4	2.0	tr	tr	tr	tr
Amphipoda	1.6	2.7	2.0	2.9	1.0	1.3	0.1	0.1	-	-

^a Macro categories include unidentified items at higher taxonomic levels.

^b Excluding scats with volumetric proportions <0.5% to minimize inclusion of hairs from grooming.

Table 2-2. Abbreviated name and description of factors included in generalized additive mixed models to the body condition (TH:HTL) of adult female brown bears in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan.

Abbreviated factor name	Description
<i>Stage 1</i>	
Year	Categorical year from 2012 to 2018.
P _L F _L	Categorical factor where "1" indicates years with light consumption of both pine nuts and salmon (2012, 2015, and 2017) and "2" indicates other years (2013, 2014, 2016, and 2018).
P _H F _H	Categorical factor where "1" indicates years with heavy consumption of both pine nuts and salmon (2013, 2016, and 2018) and "2" indicates other years (2012, 2014, 2015, and 2017).
<i>Stage 2</i>	
C/Y/S	Categorical factor where "1" indicates a female was solitary, and "2" and "3" indicate she was accompanied with cubs of the year and yearlings, respectively.
CY/S	Categorical factor where "1" indicates a female was solitary and "2" indicates she was accompanied with cubs of the year or yearlings.
C/YS	Categorical factor where "1" indicates a female was solitary or accompanied with yearlings and "2" indicates she was accompanied with cubs of the year.

Table 2-3. Akaike’s information criterion corrected for small sample size (AIC_c), ΔAIC_c , and within-stage Akaike weights (w_i) for model selection for factors influencing the body condition (TH:HTL) of adult female brown bears in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan. Variables in parentheses with “s” and “re” represent smooth terms and random effects, respectively. “x” denotes interactions of two variables.

Models	AIC_c	ΔAIC_c	w_i
<i>Stage 1 (Dietary contents)</i>			
s (session × P _H F _H) + P _H F _H + re (ID)	-1207.1	0.0	0.99
s (session) + re (ID)	-1197.1	10.0	0.01
s (session × P _L F _L) + P _L F _L + re (ID)	-1195.4	11.7	0.00
s (session × Year) + Year + re (ID)	-1146.0	61.0	0.00
<i>Stage 2 (Reproductive status)</i>			
s (session) + CY/S + re (ID)	-1225.6	0.0	0.45
s (session × CY/S) + CY/S + re (ID)	-1225.0	0.6	0.33
s (session) + C/Y/S + re (ID)	-1224.2	1.4	0.22
s (session × C/Y/S) + C/Y/S + re (ID)	-1211.6	14.0	0.00
s (session) + C/YS + re (ID)	-1207.6	18.0	0.00
s (session × C/YS) + C/YS + re (ID)	-1201.2	24.5	0.00
s (session) + re (ID)	-1197.1	28.5	0.00
<i>Stage 3 (Dietary content * Reproductive status)</i>			
s (session × P _H F _H) + P _H F _H + CY/S + re (ID)	-1230.5	0.0	0.64
s (session × P _H F _H) + P _H F _H + CY/S + P _H F _H × CY/S + re (ID)	-1228.5	2.0	0.24
s (session × P _H F _H) + CY/S + re (ID)	-1225.8	4.7	0.06
s (session) + CY/S + re (ID)	-1225.6	4.9	0.06
s (session) + P _H F _H + re (ID)	-1207.4	23.1	0.00
s (session × P _H F _H) + P _H F _H + re (ID)	-1207.1	23.4	0.00
s (session) + re (ID)	-1197.1	33.4	0.00
s (session × P _H F _H) + re (ID)	-1195.4	35.0	0.00

Table 2-4. Summary of parameter estimates for the final best-fit generalized additive mixed model fit to the body condition (TH:HTL) of adult female brown bears in the Rusha area. A significant *F* indicates nonlinearity. *edf* = estimated degrees of freedom. *n* = total number of bear-session. Bears = total number of individuals (this number was not equal throughout the period of the model).

Variable	Parameter estimates				Significance of smooth term			<i>R</i> ² _{adj}	<i>n</i>	Bears
	<i>β</i>	<i>SE</i>	<i>t</i>	<i>p</i>	<i>edf</i>	<i>F</i> _{<i>edf, d.f.</i>}	<i>p</i> (> <i>t</i>)			
								0.615	314	12
Intercept	0.684	0.006	111.57	<0.001						
Diet (low salmon consumption)	-0.009	0.004	-2.61	0.009						
Reproductive status (with offspring)	-0.020	0.004	-5.16	<0.001						
Session × diet (high pine nut and salmon consumption)					3.89	44.18	<0.001			
Session × diet (low salmon consumption)					5.61	32.94	<0.001			

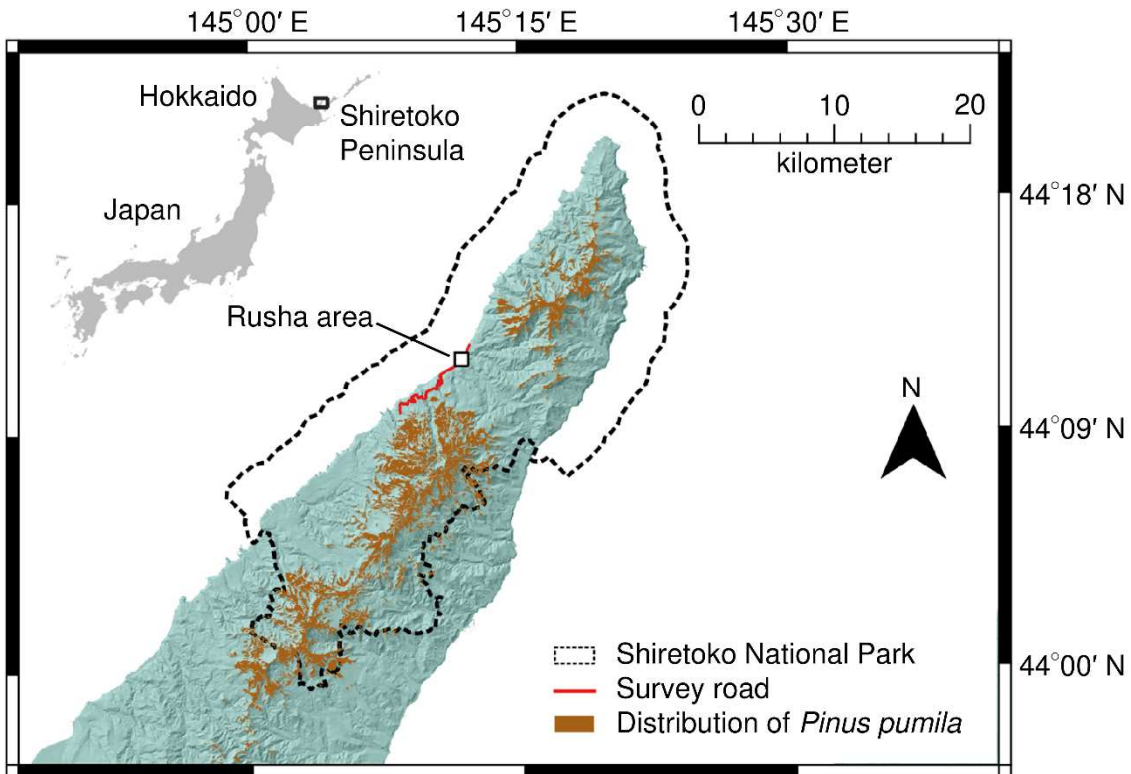


Figure 2-1. Map of the Shiretoko Peninsula, Hokkaido, Japan. This map was created using QGIS version 3.14.1 (QGIS Development Team, 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>) and edited by the author. The topographic features are based on the National Land Numerical Information published by Ministry of Land, Infrastructure, Transport, and Tourism of Japan (available from <http://nlftp.mlit.go.jp/ksj/index.html>, accessed 25-Sep-2020). The vegetation is modified from GIS data of 1:25,000 scale vegetation map created by Biodiversity Center of Japan, Ministry of the Environment (available from <http://gis.biodic.go.jp/webgis/sc-023.html>, accessed 25-Sep-2020).

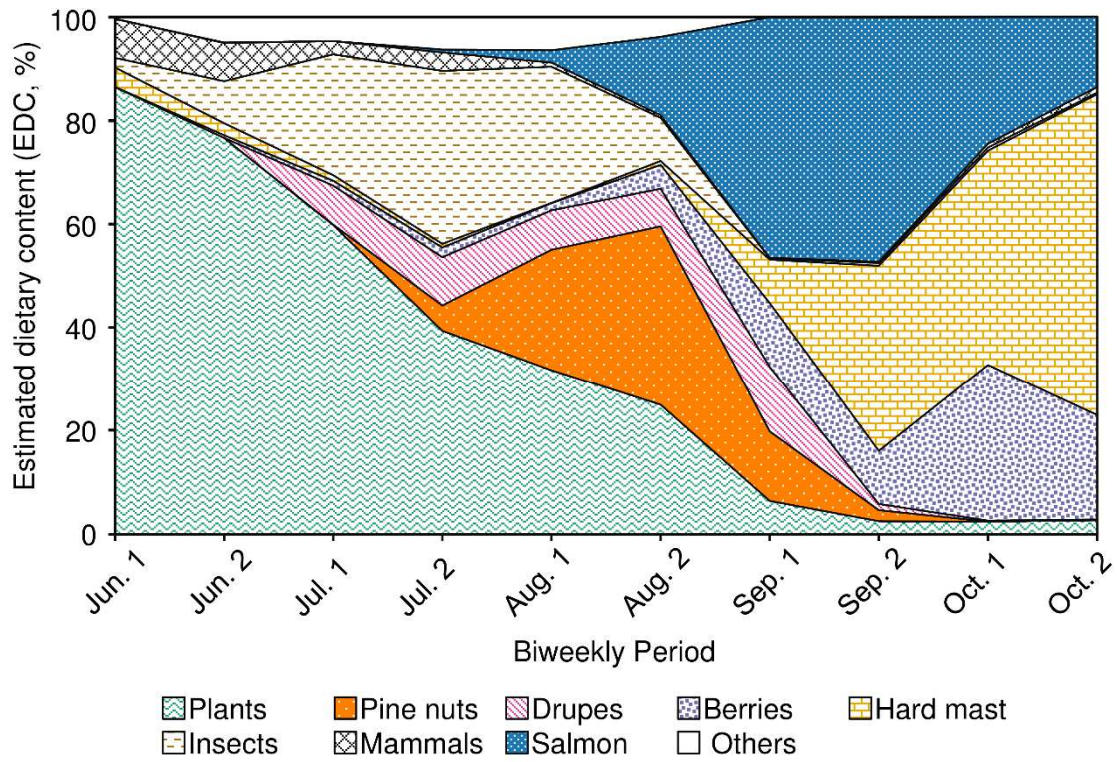


Figure 2-2. Seasonal variation in the estimated dietary content (EDC) of 1,764 brown bear scat samples collected in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan during 2013–2018.

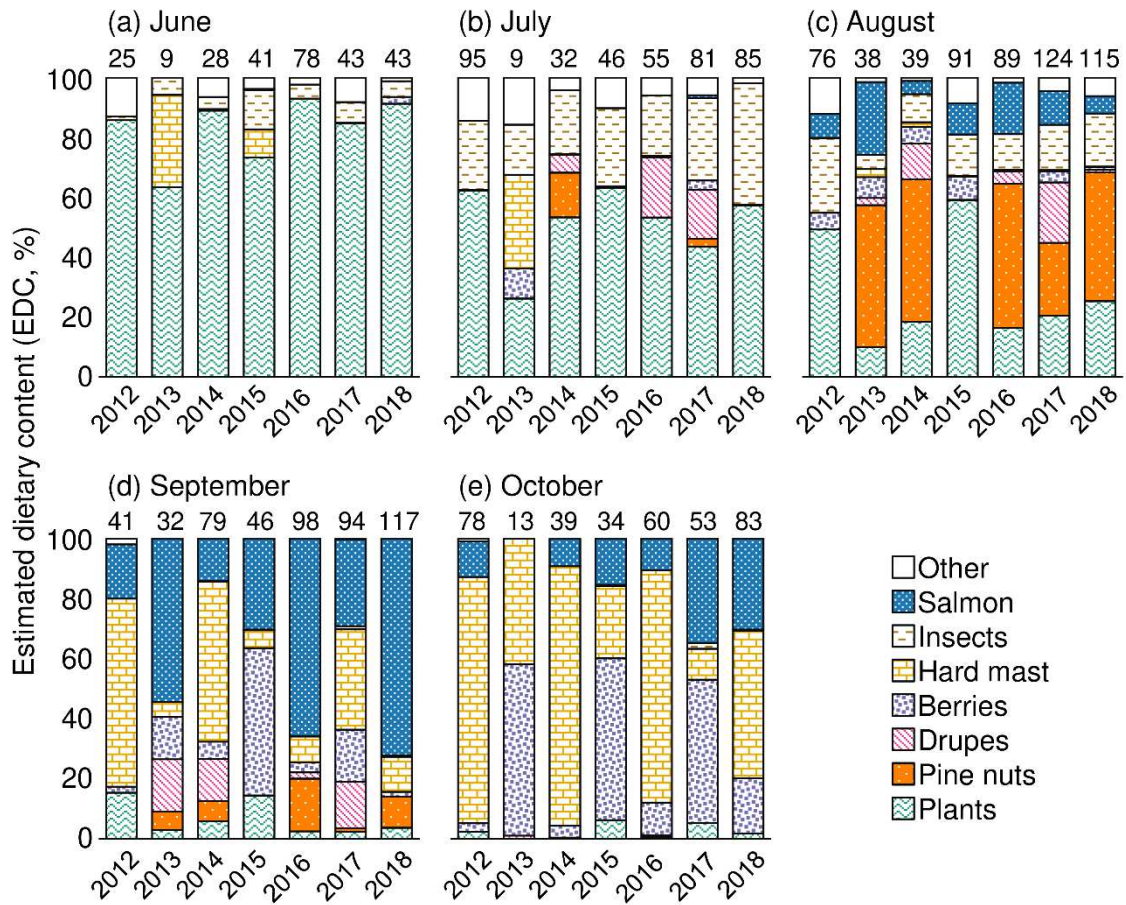


Figure 2-3. Annual variation in the estimated dietary content (EDC) of 2,079 brown bear scat samples collected in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan during 2012–2018. The numbers above the figure represent the number of scat samples.

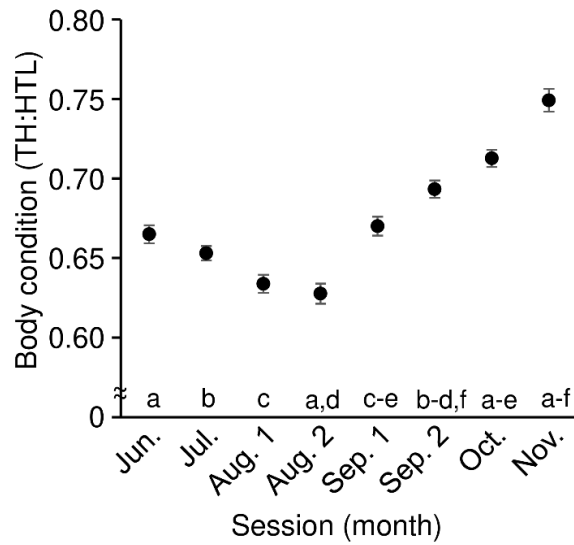


Figure 2-4. The mean body condition (TH:HTL) of adult female brown bears in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan during 2012–2018. Differences in TH:HTL among sessions were examined with a generalized linear mixed-effects model with a *post hoc* Bonferroni multiple comparison test. The same letters indicate significant differences ($p < 0.001$).

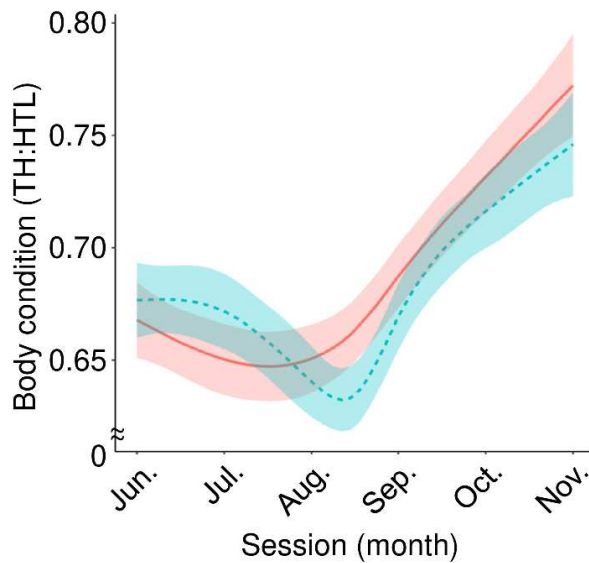


Figure 2-5. Seasonal changes in body condition predicted by generalized additive mixed models for adult female brown bears in the Rusha area of the Shiretoko Peninsula, Hokkaido, Japan. This figure shows the case in which the categorical factor for reproductive status is solitary. The red solid line indicates heavy consumption of both pine nuts and salmon, whereas the blue dotted line indicates light salmon consumption. Lines represent mean estimates, and shaded regions represent 95% confidence intervals.

FLUCTUATION IN DIET AND BODY CONDITION

Appendix 2-A. Correction factors, CF_D and CF_E , used to calculate estimated dietary content and estimated digestible energy content for brown bear diet in the Rusha area of the Shiretoko Peninsula, eastern Hokkaido, Japan.

Item	CF_D	Reference	CF_E	Reference
Plants	0.26	Hewitt and Robinson 1996; Dahle et al. 1998; Persson et al. 2001	8.4	Dahle et al. 1998; Persson et al. 2001
Pine nuts				
<i>Pinus</i> spp.	1.54	Hewitt and Robbins 1996	26.7	Pritchard and Robbins 1990
Drupes				
<i>Prunus</i> spp.	1.93	Bojarska and Selva 2013	18.1	Pritchard and Robbins 1990
Berries			18.1	Pritchard and Robbins 1990
<i>Vaccinium</i> spp.	0.54	Hewitt and Robbins 1996		
Other fleshy fruits	0.93	Hewitt and Robbins 1996		
Hard mast and nuts	1.54	the same correction factor as for pine nuts was used	26.7	the same correction factor as for pine nuts was used
Mammals			19.3	Mealey 1980; Persson et al. 2001; Stenset et al. 2016
Ungulate	1.75	Persson et al. 2001		
Large mammals	2.00	Persson et al. 2001		
Salmon				
<i>Oncorhynchus</i> spp.	40.80	Hewitt and Robbins 1996	17.6	Mealey 1980
Insects	1.10	Hewitt and Robbins 1996	-	
Formicidae			17.7	Dahle et al. 1998; Persson et al. 2001; Ciucci et al. 2014
Other insects			11.3	Dahle et al. 1998; Ciucci et al. 2014
Other				
Fungi	0.26	Stenset et al. 2016	10.0	Dahle et al. 1998
Birds	1.50	Dahle et al. 1998; Persson et al. 2001	18.8	Dahle et al. 1998; Persson et al. 2001
Shellfish	1.10	the same correction factor as for insects was used	11.3	the same correction factor as for insects was used
Amphipod	1.10	the same correction factor as for insects was used	11.3	the same correction factor as for insects was used

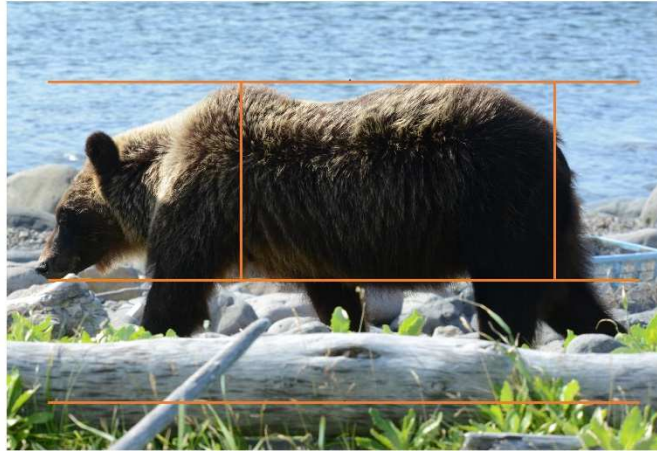
Appendix 2-B. Definition of grades (scores) used for each photograph attribute to select photographs for assessing body condition. This table was created based on a table in Shirane et al. 2020.

Attribute	Score 1 (good)	Score 2 (medium)	Score 3 (poor)
Photographing condition			
(A) Camera focus	The picture is sharp with the contour of the bear's body clearly visible.	The picture is blurry, but still clear enough to make out the contour of the bear's body.	The picture is too blurry to make out the contour of the bear's body.
(B) Camera tilt	The dorsal and ventral surface of the bear are vertical to the camera.	The dorsal and ventral surface of the bear deviate slightly from the vertical with the camera.	The dorsal and ventral surface of the bear deviates significantly from the vertical with the camera.
(C) Body angle	The body axis of the bear is perpendicular to the camera.	The body axis of the bear is angled slightly in the parallel plane, either back or forth.	The body axis of the bear is angled significantly in the parallel plane, either back or forth.
(D) Torso height measurability	Both the highest part of the waist and the lowest part of the abdomen are clearly visible.	The highest part of the waist or the lowest part of the abdomen is unclear or partly obscured, but can still be approximated.	The highest part of the waist and/or the lowest part of the abdomen are not visible due to another animal or object.
(E) Body/torso length measurability	The tip of nose (for HBL, EBL and PBL), the highest part of the shoulder (for PBL and HTL), and the base of tail are clearly visible.	The tip of nose, the highest part of the shoulder, or the base of tail is unclear or partly obscured, but can still be approximated.	The tip of nose, the highest part of the shoulder, and/or the base of tail are not visible due to another animal or object.
Bear posture			
(A) Body arch	No visible arching of the body. The bear stands parallel to the ground.	-	The legs or the central part of the body is significantly lifted or dropped.
(B) Body straightness	Right/left forelimb and hindlimb are in front of the other. The hip joint is not fully extended.	Right/left forelimb and hindlimb are inside the body or either of the legs is fully extended.	-

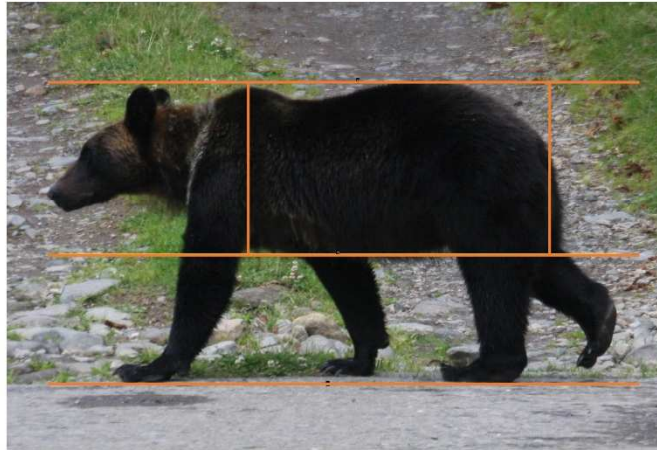
Appendix 2-C. Equation for converting the percentage fecal volume estimated visually to EDC.

Categories	Regression equation	adjusted R^2	p value
Plants	$y = 0.90x$	0.96	$p = 0.015$
Drupes	$y = 0.87x$	0.92	$p = 0.013$
Berries	$y = 0.85x$	0.96	$p < 0.001$
Hard mast	$y = 0.98x$	0.96	$p = 0.554$
Pine nuts	$y = 1.15x$	0.97	$p < 0.001$
Mammals	$y = 0.40x$	0.12	$p < 0.001$
Salmon	$y = 1.10x$	0.93	$p = 0.114$
Insects	$y = 0.96x$	0.73	$p = 0.664$

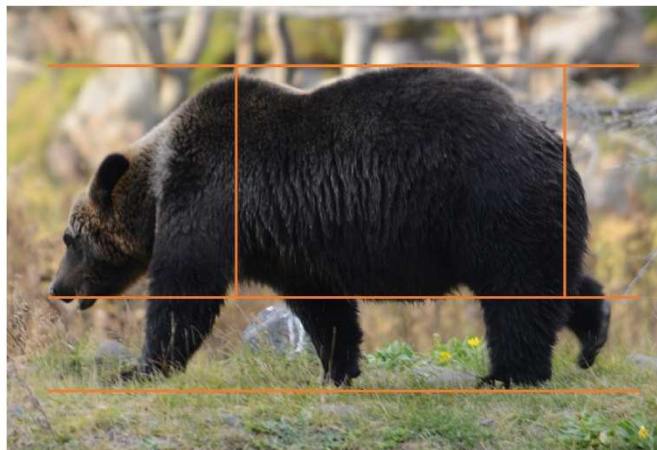
(a) June 2015, TH:HTL = 0.647



(b) Late August 2015, TH:HTL = 0.582



(c) October 2015, TH:HTL = 0.717



Appendix 2-D. An example of morphometric measurement and body condition evaluation (TH:HTL) using photographs of an adult female brown bear (bear ID: HC). These photographs were taken on (a) July 27, (b) August 23, and (c) October 7, 2015, respectively.

SUMMARY

Body condition in mammals fluctuates depending on energy intake and expenditure. Although brown bears (*Ursus arctos*) inhabiting the Shiretoko Peninsula in Hokkaido have access to various high-energy foods, malnutrition due to summer food shortages may lead to bear intrusion into residential areas, which often result in the removal of bears as nuisances. To assess seasonal and annual fluctuation in the body condition of adult female brown bears in relation to diet and reproductive status, a longitudinal study was conducted in a special wildlife protection area on the Shiretoko Peninsula during 2012–2018. First, analyses of 2,079 bear scats revealed that pine nuts accounted for 39.8% of energy intake in August and salmon accounted for 46.1% in September and that their consumption by bears varied annually. Second, the ratio of torso height to torso length was calculated as an index of body condition from 1,226 photographs of 12 adult females. Results indicated that body condition continued to decline until late August and started to increase in September when salmon consumption increased. In addition, body condition began to recover earlier in years when consumption of both pine nuts and salmon was high. Furthermore, females with offspring had poorer body condition than solitary females, in particular in late August in years with light salmon consumption. Our findings suggest that coastal and subalpine foods, which are unique to the Shiretoko Peninsula, determine the summer body condition of female brown bears as well as their survival and reproductive success.

CHAPTER 3

An investigation of restricted mountain climbing
and salmon fishing among female brown bears
with dependent young in Hokkaido, Japan

INTRODUCTION

Animal movement is determined by energetic costs associated with acquiring resources. In addition to food availability, factors such as reproductive status, den site availability, or avoidance of conspecifics or predators can affect the movement of individuals (Nathan et al. 2008). Environmental characteristics such as reproductive period, air temperature, and daylight length are also important for understanding the seasonality of animal movement (Nielsen et al. 2006; Ware et al. 2013). Because these factors can affect individual fitness parameters and population growth rates, recognizing space-use strategies is important for understanding species population dynamics and for decision making in management and conservation.

Brown bear movement patterns are driven by their complex life history (Pop et al. 2018a) and influenced by seasonality and annual variation in food availability, which play important roles in activity and habitat selection (Frąckowiak et al. 2014; Munro et al. 2006; Pop et al. 2018b). A previous study showed that the strength and duration of berry selection by bears varied depending on precipitation and associated food availability (McClelland et al. 2020). Annual variation in hard mast production has been linked to changes in bear survival rate (Schwartz et al. 2006) and movement (Blanchard and Knight 1991; Gunther et al. 2004). Similarly, American black bears have been reported to increase their home range size or movement in years with poor mast food production (Kasbohm et al. 1998), leading to bears using areas with high human density (Baruch-Mordo et al. 2014). By contrast, another study suggested that mast production does not determine movement behavior in Scandinavian brown bear population (Hertel et al. 2019).

Breeding strategies are also linked to bear behavior. Brown bears have a promiscuous mating system (Schwartz et al. 2003a; Steyaert et al. 2012), and the mating season persists from late spring until early summer (Craighead et al. 1995; Spady et al. 2007). Infanticide can be a reproductive strategy for males as it leads to increased breeding opportunities with females (Hrdy 1979). In Sweden, where infanticide by adult male bears is common, mothers accompanied by cubs reduce their home range size and movement distances to avoid encounters with adult males (Dahle and Swenson 2003b; Martin et al. 2013; Steyaert et al. 2014). By contrast, most cub disappearances in brown bear populations on the Shiretoko Peninsula, Hokkaido, Japan, occur in July and August, which suggests that the main cause of cub mortality is body condition deterioration in summer (Shimozuru et al. 2017). Thus, the behaviors of female bears with cubs may differ among populations.

A previous study reported in Chapter 2 has found that annual variation in pine nut and

salmon consumption determines bear body condition in summer, and that female bears with dependent offspring have poorer body condition than do solitary females. Possible reasons for these phenomena include high energy consumption by the mother for raising offspring (Hilderbrand et al. 2000; Wright et al. 1999) or low offspring mobility (Martin et al. 2013; Steyaert et al. 2014), which reduces opportunities for exploring food resources, in turn reducing energy intake. Although Chapter 2 that investigated scat contents on the Shiretoko Peninsula have reported that brown bears frequently travel between the subalpine region and the coastline for foraging, it remains unknown whether such movement is possible for females with cubs. It is also unclear how annual diet variation affects the movement patterns of bears.

The objective of the present study was to clarify the movement ecology of adult female brown bears on the Shiretoko Peninsula. Using Global Positioning System (GPS) location data during 2014–2020, I examined changes in female bear behavior according to reproductive status and summer diet. I hypothesized that females with cubs would not select their regular resources due to movement restrictions imposed by poor cub mobility and the risk of infanticide. First, I tested whether female bears with offspring move more slowly compared to solitary females, including terrain elements such as vegetation and slope as explanatory variables to examine movement restrictions on female bears with offspring. Next, I investigated seasonal habitat selectivity and determined whether the vegetation selected by bears differed according to reproductive status, focusing on the alpine stone pine community. I also created models for high and low pine nut and salmon consumption to test whether habitat selectivity changed depending on dietary content. Finally, I examined whether the probability of bears visiting salmon spawning sites during specific periods of the day depended on reproductive status.

MATERIALS AND METHODS

Ethical approval

Field experiments were approved by Hokkaido Regional Environment Office and Kushiro Nature Conservation Office (Permit Number: 1606091, 1705182, and 1905131). All procedures were conducted in accordance with the Guidelines for Animal Care and Use of Hokkaido University (Permit Number: 15009 and 17005) and were approved by the Animal Care and Use Committee of the Graduate School of Veterinary Medicine, Hokkaido University (Permit Number: 1152, 15009, and 17005).

Study area

This study was conducted in the Rusha area, near the tip of the Shiretoko Peninsula (Fig. 3-1), Hokkaido, Japan. The Rusha area is a narrow estuarine coast stretching south to north for approximately 3 km and has been designated as a special wildlife protection area where public access is prohibited without permission.

The year was divided into three biological seasons, each corresponding to particular foraging behaviors reported in Chapter 2. During early summer (16 June–15 July), the bear diet is mainly composed of herbaceous plants and ants. In late summer (16 July–31 August), the nutritional values of herbaceous plants decrease (Cicnjak et al. 1987) and berries are still immature; therefore, bear diets are dominated by Japanese stone pine nuts and salmon. In autumn (1 September–15 October), bears consume energy-rich foods such as salmon, acorns, and berries to fatten before entering the winter den for hibernation.

Food habit

Bear scats were collected in the Rusha area and along survey roads leading to the area from June to November in each year during 2014–2020. Percent volume of each food item was estimated visually (vFV), and the time from defecation to scat collection was also estimated based on freshness in relation to recent weather conditions. Because major consumption period of pine nuts and salmon is August and September, respectively (see Chapter 2), only scats excreted in August and September were used in the subsequent analysis. Scats encountered during 2014–2018 were collected, and those contents were analyzed using the point-frame method (Sato et al. 2000). All scat samples were washed through a sieve (1.0-mm mesh) and materials remaining on the sieve were evenly spread on a lab tray marked with a 1 cm grid. Each food item lying on points of intersection on the tray was identified, and the percent volume for each food item was calculated by dividing the number of points on which each item lay by the total number of points covered with all food items contained in the sample. The corresponding correction factors (CFD, see Appendix A for details; Hewitt and Robbins 1996; Dahle et al. 1998; Persson et al. 2001; Bojarska and Selva 2013; Stenset et al. 2016) were used to calculate estimated dietary content (EDC). In addition, the vFV obtained in 2019 and 2020 was equated to EDC based on the regression equations reported in Chapter 2. Then, years were classified as either heavy or light for bear use of pine nuts depending on whether its EDC value in August exceeded mean EDC.

Individual tracking data

Seven adult female brown bears (≥ 5 years old; bear ID: DR, GI, KR, KS, LI, RI, and WK) were immobilized in July or August during 2014–2018 using a remotely injected dose of medetomidine hydrochloride (Dorbene® Vet, Kyoritsu Seiyaku Co., Ltd., Tokyo, Japan) and

tiletamine–zolazepam (Zoletil®, Virbac S.A., Carros, France). For an individual weighing 100 kg, a solution of an anesthetic drugs containing 7.5 mg medetomidine and 550 mg tiletamine–zolazepam was prepared. This drug combination has been previously reported to be safe and reliable for anesthetizing free-ranging brown bears (Fandos Esteruelas et al. 2017). The anesthetic combination was administered using 5-mL syringe darts with 1.5×25 mm barbed needles with side ports (DAN-INJECT®; Dan-Inject ApS, Kolding, Denmark), using a CO₂ injection rifle (DAN-INJECT® Model J.M.ST. or J.M.DB.13) from a distance of 20–25 m.

During immobilization, GPS transmitter collars (VECTRONIC Aerospace GmbH, Berlin, Germany; and Lotek, Aurora, Ontario, Canada) were deployed on individual bears. The GPS transmitters were programmed to record locations at a fixed frequency of 2 h (*i.e.*, 12 daily locations). Location errors are inherent with this type of data and can induce bias in habitat analysis. Therefore, I eliminated potentially large location errors via data screening, in which I removed two-dimensional (2D) and three-dimensional (3D) fixes showing positional dilution of precision (PDOP) values >5 and >15 , respectively.

The reproductive status of the tracked bears was determined from direct observations conducted during periodic surveys (≥ 1 day/2 weeks) of the Rusha area during 2014–2020. The seven captured individuals were easily identified by their appearance (*e.g.*, size, color, facial characteristics, chest markings, and ear tags) (Shimozuru et al. 2017) and were frequently observed in the Rusha area throughout the surveillance period. The bears were classified into three reproductive groups: females with cubs of the year, females with yearlings, and lone females. When a cub disappeared from its mother, the cub was considered dead, as in other studies (Miller et al. 2003; Shimozuru et al. 2017; Swenson et al. 2001). The probability of litter loss is related to the rate of maternal movement, and the movement pattern of females after litter loss shifts to that of lone females within 1–2 days (Gardner et al. 2014; Steyaert et al. 2014). Therefore, one bear-year (KR2015), which lost a cub in August, was not used in this study.

Habitat environmental data

The study area was divided into a grid of pixels (10 m \times 10 m), each were characterized for three variables: vegetation, slope, and distance to salmon spawning site. I classified four vegetation types using vegetation survey results conducted by Biodiversity Center of Japan: alpine shrub community (mainly Japanese stone pine), coniferous forest (mainly *Picea glehnii* and *Abies sachalinensis*), deciduous (mainly birch *Betula ermanii*) and mixed forest (mix of coniferous and deciduous forest), and grassland. I derived slopes from a digital elevation model of the study area (10 m contour line, The Geospatial Information Authority of Japan). I used the map of river from the National Land Numerical Information published by Ministry of Land,

Infrastructure, Transport, and Tourism of Japan to create a map of salmon spawning sites. Using the upper limit of the Hokkaido salmon run (Urabe et al. 2013), I defined a salmon spawning site as any part of a river where the altitude was ≤ 100 m. QGIS version 3.14.1 (QGIS Development Team 2020) was used for preliminary preparation of environmental data.

Movement velocity

To estimate daily movement patterns, the distance and time between successive locations was used to measure movement rates. For each female, movements were characterized independently in discrete segments connecting successive locations. Movement speed between locations was estimated by dividing segment lengths (or Euclidean distances between consecutive locations) by the time lag separating the locations (*i.e.*, 2 hours). To avoid bias resulting from missing data, I removed speed estimates that were obtained from any two locations separated by one or more missing data points. For computational convenience, I used only 1 day per every 3 days. Analyses were carried out using R (R Core Team 2020) and the package “adehabitatLT” (Calenge 2006).

Resource selection function (RSF) model

The habitat selection of individuals was assessed within group-level home ranges (second- and third order selection, Johnson 1980). Relative frequency of use was used as the response variable in an RSF framework (Manly et al. 1972) to model the probability of use for each bear as a function of environmental predictor variables (Marzluff et al. 2004). To achieve the largest home range size for this brown bear population, a multiyear (2014–2020) 100% minimum convex polygon (MCP) was constructed using the movement data of all individuals. The part of the MCP home range that overlaps with the open water area was removed. Then, random points were generated as available points comprising a subset of all GPS locations across 6 years within the MCP home range. MCP home range was estimated using the package “adehabitatHR” (Calenge 2006) in R.

Stream visitation pattern

To describe the daily pattern of salmon foraging by bears, this study assumed that individuals were exploiting salmon only when their GPS locations were within 50 m of a salmon spawning site, following the method of a previous study (Deacy et al. 2016). Each location was categorized into one of three daily periods: daytime (daylight), night-time (darkness), twilight (dusk and dawn, on average, at 3:30 and 19:00 in early summer, 4:30 and 18:30 in late summer, and 5:30 and 17:00 in autumn, respectively). For each bear, I calculated the probability that bears

would visit a salmon spawning site during each monitored hour (*i.e.*, every 2 h) by summing the number of visits to the spawning site for every hour and dividing the result by the total number of locations per hour.

Statistical analyses

Generalized additive mixed models (GAMMs) were used to assess the effects of time (in hours), reproductive status, vegetation type (alpine shrub community, coniferous forest, deciduous and mixed forest, and grassland), and slope (in degrees) on movement velocity in km/h. A GAMM is a flexible semi-parametric method for modeling both linear and nonlinear relationships between a response variable and its explanatory variables. A cyclic cubic spline smoother was used to model the nonlinear and cyclic effect of time of day, where the point at the end of a given day is constrained to be the same as that at the beginning. I included bear-year as a random factor. Due to the strong effect of time found in previous bear activity studies (Kaczensky et al. 2006; Moe et al. 2007), I assumed that a null model without daytime would not have biological meaning. Therefore, I included daytime in all models. The most parsimonious model was selected from all possible combinations of the aforementioned variables based on the Akaike information criterion (AIC). The “mgcv” (Wood 2011) and “MuMIn” (Bartoń 2020) packages were used in R.

To test which habitat characteristics influenced brown bear habitat selection, I compared bear telemetry locations with random points using mixed-effect logistic regression with binomial distribution and a logit-link function with a binary response variable (1: bear telemetry location, 0: random point). These models predict the relative probabilities that a point is a bear location and not a random location based on habitat variables. Vegetation type was used as an explanatory variable in this analysis. Because habitat selection can change with seasonal resource availability (McClelland et al. 2020) and annual food production (Costello et al. 2014), I generated a separate model for each season; I generated separate models for late summer and autumn depending on whether pine nuts and salmon consumption were high or not.

To test the hypothesis that bears would visit streams less frequently when accompanied by offspring, I used a linear mixed effect model with the probability of bears visiting salmon spawning sites as the dependent variable, and time period, reproductive status, and their interaction as the independent variables; bear-year was the random intercept. The Bonferroni correction was used to evaluate differences in mean values between seasons, time periods, and reproductive statuses.

RESULTS

Food habit

Food items were analyzed from 1,140 scats collected during 2014–2020 (118, 137, 187, 218, 212, 173, and 95 for each year, respectively). The mean EDC of pine nuts in August for 7 years was $30.8\% \pm 20.0$ (standard deviation), and EDC was 47.5, 0.0, 47.3, 24.3, 42.9, 3.6, and 49.7 for each year, respectively. Based on these results, years were divided into 2 groups: 2014, 2016, 2018, and 2020 were years with high consumption of pine nuts; and the others were years with low pine nuts consumption. The mean EDC of salmon in September for 7 years was $37.3\% \pm 23.7$, and EDC was 14.1, 30.2, 65.4, 28.9, 72.2, 3.0, and 47.6 for each year, respectively. Based on these results, years were divided into 2 groups: 2016, 2018, and 2020 were years with high consumption of salmon; and others were years with low salmon consumption.

Movement velocity

This study obtained 23,479 GPS location data from seven females (Table 3-1). Biological factors including season, reproductive status, and their interaction affected hourly speed (Table 3-2). Brown bears exhibited a circadian movement pattern, with peaks around dawn and dusk (Fig. 3-2). Solitary females traveled at the highest speed at 1–2 h after sunrise and 1–2 h before sunset (Fig. 3-2). During late summer, the first peak was higher than the second peak in solitary females, and the second peak was higher than the first peak in early summer and autumn. By contrast, females with cubs exhibited a single peak around noon in early summer. On average, solitary females moved at a speed of 0.29 km/h. Females with cubs moved more slowly than did solitary females during the first two seasons of the year (0.23 km/h and 0.25 km/h during early summer and late summer, respectively). Females with yearlings exhibited the same pattern as did solitary females, but their travel speeds had a wider confidence interval due to the small number of tracked individuals and large differences among individuals.

The best model revealed that terrain factors including vegetation, slope, and their seasonal interaction affected hourly velocity (Table 3-2). Bears reduced their movement velocity in steep areas (-0.003 ± 0.00 , mean \pm SE) and in deciduous and mixed forest, coniferous forest, and alpine regions (Fig. 3-3). Notably, movement velocity was much slower in alpine shrub communities among bears of any reproductive status. This effect tended to be larger in females with cubs, although the difference between females with and without cubs was not significant.

Habitat selection

In early summer and autumn, bears strongly avoided alpine shrub communities (-5.67 ± 2.25 and -4.06 ± 1.93 , respectively; Table 3-3 and 3-5; Fig. 3-4). During late summer, when pine nut consumption was high, bears selected alpine shrub communities (0.79 ± 0.20 ; Table 3-4; Fig. 3-4) and avoided deciduous and mixed forest (-0.54 ± 0.11) and coniferous forest (-1.05 ± 0.39). By contrast, during late summer, when pine nut consumption was low, there was no significant selectivity for alpine shrub communities; instead, bears tended to avoid alpine regions (-3.24 ± 1.67). In autumn, there was no significant difference between years with high and low salmon consumption.

In terms of individual differences, bears with cubs tended to avoid alpine shrub communities and grasslands more strongly than did solitary females in early summer (Fig. 3-5). However, in late summer, when pine nut consumption was high, one female with cubs (Bear-year: KS2016) selected alpine regions in the same way that solitary females did (Fig. 3-6), whereas two females with yearlings (LI2016 and GI2020) exhibited relatively low alpine region selectivity. In years with low pine nut consumption, females with cubs strongly avoided alpine regions in late summer. Overall, there were large individual differences in habitat selectivity (Fig. 3-5, 3-6, and 3-7).

Stream visitation patterns

The probability of bears visiting salmon spawning sites was affected by season, time period, and reproductive status ($p < 0.001$). No differences in the time period of spawning site visitation were observed for solitary females in early or late summer, but they spent more time at the salmon spawning site in daytime than at night in autumn ($p = 0.046$; Fig. 3-8). The probability of spawning site visitation was higher during the day and at twilight in autumn than in early summer ($p = 0.001$ and 0.005 , respectively). All other comparisons, including between different reproductive statuses, produced no significant differences ($p \geq 0.05$), although females with cubs were more likely to visit the river during the day than at night or twilight in autumn.

DISCUSSION

Bear movement velocity was lower in early and late summer for females with cubs than for solitary females; this difference became smaller in autumn. This result is likely due to low cub mobility, and therefore, the difference decreases as cubs acquire greater mobility in autumn. Solitary females exhibited crepuscular diurnal activity, and females with cubs were active during the day. Brown bear maternal care strategies include reducing movement (*i.e.*, smaller home

ranges) during spring and early summer, displaying more diurnal behavior, and the spatial segregation of adult females accompanied by cubs. Such strategies have been observed in several European and North American populations (Martin et al. 2013; Ordiz et al. 2007; Steyaert et al. 2012, 2014). In Sweden, infanticide by adult males is the main cause of cub mortality, and females with cubs are active during the day to avoid encounters with adult males (Martin et al. 2013; Steyaert et al. 2014). Even on the Shiretoko Peninsula, where cub mortality due to infanticide is considered rare (Shimozuru et al. 2017), females are thought to be more active during the day to avoid adult males or other conspecifics.

Terrain factors also affected bear movement velocity, resulting in slow travel by females in alpine and steep areas, likely driven by the difficulty of traversing the topography or bears remaining in a specific place for foraging or resting behavior (Martin et al. 2013). The results of this study showed that movement velocity was lowest in the alpine region in early summer, when pine nuts are not available, suggesting that this result was caused by restricted movement rather than foraging behavior. It was expected that females with cubs would be more susceptible to such topographical movement restrictions; however, there was no difference in movement restriction between female bears with and without offspring.

Females with cubs tended to select forests over grasslands during early summer, whereas lone females and females with yearlings selected grasslands. Females with cubs settled in potentially safe areas during the first few months after den emergence, when cubs are most vulnerable (Penteriani et al. 2020). Safe areas for bears are often inaccessible places such as cliffs, which provide shelter from both conspecifics and human activity. By contrast, in Scandinavia, females with cubs select areas in relatively close proximity to human settlements that are avoided by adult males, suggesting that human-related landscape variables act locally as a protective shield for females with cubs (Steyaert et al. 2016). In the study area of this study, most of the grasslands were located in open areas by the sea, near forest roads used by fishermen and researchers. Therefore, I expected that the grasslands would be selected to avoid adult males; however, the result was contrary to expectation. This study obtained data for three individual females with cubs in early summer (ID: GI, KS, and WK). Among these, bears GI and KS were less likely to be observed in coastline grasslands than other individuals, probably because they spent more time in forests, regardless of reproductive status. To determine whether these bears selected forests as safe areas or avoided grasslands as dangerous areas, further studies investigating whether grasslands are selected when accompanied by offspring in individuals frequently observed along the coastline is required.

The RSF models showed that female bears strongly selected alpine shrub communities in years with high pine nut consumption. Contrary to the that bears with offspring would be

restricted from moving to high-altitude regions, one female with a cub selected such regions. Although the result of moving velocities indicated that females with cubs were generally restricted in movement in late summer compared to solitary females, it appears possible for females with cubs to visit alpine regions.

There was no significant difference in the probability of salmon exploration among females of different reproductive status. Although bears are usually diurnal or crepuscular, they are thought to shift their activity patterns so as to forage for salmon in the dark to avoid other bear species and people (Klinka and Reimchen 2009; Olson et al. 1998). Brown bears in the Rusha area mainly visited salmon spawning sites during daytime because they have perhaps no conflicts with humans or other animals. In Alaska, females with cubs tend to avoid salmon spawning streams to reduce encounters with adult males, which may lead to lower body mass and lower cub survival (Ben-David et al. 2004). In the study area of this study, females are highly habituated to humans, while males are probably less habituated. As a result, it is rare to observe adult male bears foraging for fish during the day, suggesting that the males prey on salmon at night. Thus, daytime salmon exploration by females in this study may suggest temporal isolation of feeding activities from males.

For many wild species, movement decisions and habitat use are important determinants of overall energetic balance (Brown et al. 2004), and optimal foraging theory predicts that animals may minimize their energy expenditure relative to energy intake (Pyke et al. 1977). Because pine nut availability data were not available for the Shiretoko Peninsula, I assumed that nut production was low in years when pine nut consumption was low. According to this assumption, bears could be predicted to have taken one of three strategies to maintain energy balance: 1) bears explore alpine regions extensively to obtain pine nuts, which are the only high-nutritional food available in August; 2) bears explore forests and grasslands for alternative food sources such as ants and immature berries; and 3) bears reduce energy expenditure by reducing movement, and wait for salmon spawning before increasing movement. The RSF models showed that bears tended to avoid alpine shrub communities and significantly avoided forest habitats. This result suggests that bears may not actively seek pine nuts or alternative fruits when pine nuts are scarce, that is, the third strategy is partially supported. In several bear species and populations, bears increase their movement activity (Koike et al. 2012), home range size (Kozakai et al. 2011), and human settlement use (Johnson et al. 2015) in response to poor mast production. In addition, several human-modified landscapes such as agricultural landscapes and areas close to human settlements with abundant fruit can act as ecological traps that lead to maladaptive habitat selection (Lamb et al. 2017; Penteriani et al. 2018). However, in regions such as the Rusha area, where there is no artificial food nearby and high-nutritional foods such as salmon are available every year, brown

bears may reduce their energy expenditure and endure hunger until the salmon run. To clarify the natural responses of brown bears to annual fluctuations in food resources, it is necessary to further study their changes in energy expenditure.

CONCLUSIONS

This study determined that female brown bears on the Shiretoko Peninsula, Hokkaido, Japan change their behavior depending on reproductive status and summer diet. Females with cubs were restricted in movement; however, the use of alpine regions and salmon spawning sites by mothers was not significantly different from that of solitary females. A previous study reported in Chapter 2 revealed that brown bear body condition declined continually from June to late August and that females with offspring had poorer body condition than did solitary females. Together with the results of the present study, these findings indicate that although energy intake may be reduced due to behavioral restrictions, increased energy expenditure due to cub rearing is probably a greater factor leading to poor body condition. In addition, the RSF models showed that brown bears used different areas depending on food condition in summer. Brown bears in the Rusha area ate abundant salmon even when pine nut production was poor, whereas not all bears had access to salmon throughout the peninsula. To clarify the factors driving human–bear conflicts on the Shiretoko Peninsula, it is necessary to further study regional and individual differences in the feeding habits, food availability, and behavioral responses of brown bears.

Table 3-1. Summary of GPS locations from each individual brown bear included in the study in the Shiretoko Peninsula, Hokkaido, Japan. Reproductive status of bears is noted: S, solitary females; C, females with cubs; and Y, females with yearlings. “Date.begin” and “Date.end” refer the date and time of the first and last position used for each individual, respectively.

Bear-year	Status	N. of locations	Date.begin		Date.end	
DR2014	C	705	2014/9/1	0:00:00	2014/10/31	22:01:00
DR2015	S	1763	2015/6/1	0:00:00	2015/10/31	22:00:00
DR2016	S	1702	2016/6/1	0:00:00	2016/10/31	20:00:00
DR2017	S	1783	2017/6/1	0:00:00	2017/10/31	22:00:00
DR2018	S	830	2018/6/1	0:00:00	2018/8/13	10:00:00
GI2015	C	1633	2015/6/1	0:03:00	2015/10/31	22:00:00
GI2016	S	1415	2016/6/1	2:03:00	2016/10/12	8:01:00
GI2018	S	700	2018/9/1	0:01:00	2018/10/31	22:00:00
GI2019	C	1759	2019/6/1	0:00:00	2019/10/31	22:00:00
GI2020	Y	1081	2020/6/1	0:00:00	2020/8/31	22:00:00
KR2014	S	702	2014/9/1	0:00:00	2014/10/31	22:00:00
KR2016	S	1046	2016/6/1	0:01:00	2016/8/31	22:00:00
KS2015	S	822	2015/7/16	0:00:00	2015/10/28	22:00:00
KS2016	C	1789	2016/6/1	0:01:00	2016/10/31	22:00:00
LI2016	Y	1185	2016/7/16	0:00:00	2016/10/31	22:00:00
RI2014	C	699	2014/9/1	0:00:00	2014/10/31	22:00:00
RI2015	S	1581	2015/6/1	2:00:00	2015/10/17	8:00:00
WK2018	S	1232	2018/7/16	0:00:00	2018/10/31	22:00:00
WK2019	C	1052	2019/6/1	0:03:00	2019/8/31	22:00:00

Table 3-2. Summary of the most parsimonious generalized additive mixed models used to test for differences in movement velocity among adult female brown bears with different reproductive statuses in the Shiretoko Peninsula, Hokkaido, Japan, during 2014–2020. “S” denotes Solitary females, “C” denotes females with cubs, and “Y” denotes females with yearlings. “:” denotes interactions. Variables in parentheses with “s” represent smooth terms.

Variables	Estimate	SE	<i>t</i>	<i>p</i>-value
(Intercept)	0.306	0.018	16.94	<0.001
Late summer	-0.025	0.017	-1.51	0.132
Autumn	-0.056	0.017	-3.30	0.001
C	-0.040	0.030	-1.37	0.170
Y	-0.083	0.039	-2.12	0.034
Deciduous&Mixed forest	-0.081	0.015	-5.49	<0.001
Coniferous forest	-0.081	0.017	-4.67	<0.001
Alpine shrub community	-0.217	0.042	-5.23	<0.001
Slope	-0.003	0.000	-12.02	<0.001
Late summer:C	0.019	0.017	1.12	0.264
Autumn:C	0.072	0.017	4.26	<0.001
Late summer:Y	0.010	0.027	0.36	0.716
Autumn:Y	0.046	0.035	1.32	0.187
Late summer:Deciduous&Mixed forest	0.053	0.020	2.67	0.008
Autumn:Deciduous&Mixed forest	0.046	0.019	2.45	0.014
Late summer:Coniferous forest	0.051	0.023	2.27	0.023
Autumn:Coniferous forest	0.034	0.021	1.61	0.107
Late summer:Alpine shrub community	0.081	0.044	1.82	0.069
Autumn:Alpine shrub community	0.156	0.066	2.38	0.018
statusC:Deciduous&Mixed forest	-0.037	0.021	-1.72	0.085
statusY:Deciduous&Mixed forest	0.036	0.023	1.54	0.124
statusC:Coniferous forest	-0.032	0.023	-1.42	0.157
statusY:Coniferous forest	0.074	0.029	2.53	0.011
statusC:Alpine shrub community	-0.033	0.034	-0.95	0.342
statusY:Alpine shrub community	0.104	0.042	2.47	0.014
	edf	Ref.df	F	<i>p</i>-value
s(hour):Early summer	2E-05	8.000	0.00	0.408
s(hour):Late summer	3.651	8.000	2.11	<0.001
s(hour):Autumn	0.451	8.000	0.07	0.281
s(hour):S	6.448	8.000	42.94	<0.001
s(hour):C	4.611	8.000	14.05	<0.001
s(hour):Y	3.885	8.000	5.91	1E-11

Table 3-3. Habitat selection coefficients estimated using resource selection function (RSF) models for brown bears in early summer in the Shiretoko Peninsula, Hokkaido, Japan.

Variables	β	SE	<i>p</i>
Alpine shrub communities	-5.67	2.25	0.012
Coniferous forest	-0.47	0.23	0.043
Deciduous & mixed forest	-0.14	0.09	0.106
Grassland	0.68	0.40	0.083

Table 3-4. Habitat selection coefficients estimated using resource selection function (RSF) models for brown bears in late summer in the Shiretoko Peninsula, Hokkaido, Japan.

Variables	high			low		
	pine nuts consumption			pine nuts consumption		
	β	SE	<i>p</i>	β	SE	<i>p</i>
Alpine shrub communities	0.79	0.20	<0.001	-3.24	1.67	0.053
Coniferous forest	-1.05	0.39	0.006	-0.81	0.32	0.013
Deciduous & mixed forest	-0.54	0.11	<0.001	-0.43	0.14	0.002
Grassland	0.63	0.33	0.054	0.52	0.59	0.375

Table 3-5. Habitat selection coefficients estimated using resource selection function (RSF) models for brown bears in autumn in the Shiretoko Peninsula, Hokkaido, Japan.

Variables	high			low		
	salmon consumption			salmon consumption		
	β	SE	<i>p</i>	β	SE	<i>p</i>
Alpine shrub communities	-4.06	1.93	0.036	-4.88	1.65	0.003
Coniferous forest	-0.11	0.28	0.696	0.15	0.23	0.528
Deciduous & mixed forest	0.05	0.11	0.671	-0.02	0.09	0.805
Grassland	0.90	0.50	0.069	0.79	0.40	0.051

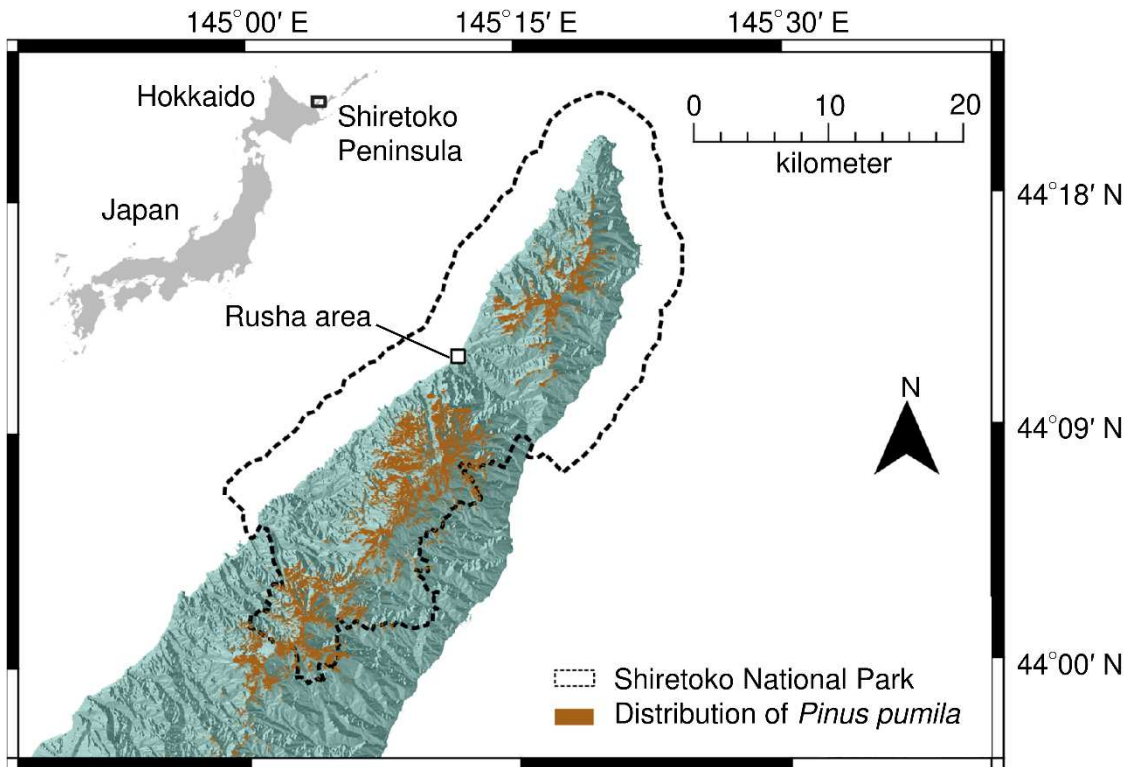


Figure 3-1. Map of the Shiretoko Peninsula, Hokkaido, Japan. This map was created using QGIS version 3.14.1 (QGIS Development Team, 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>) and edited by the author. The topographic features are based on the National Land Numerical Information published by Ministry of Land, Infrastructure, Transport, and Tourism of Japan (available from <http://nlftp.mlit.go.jp/ksj/index.html>, accessed 25-Sep-2020). The vegetation is modified from GIS data of 1:25,000 scale vegetation map created by Biodiversity Center of Japan, Ministry of the Environment (available from <http://gis.biodic.go.jp/webgis/sc-023.html>, accessed 25-Sep-2020).

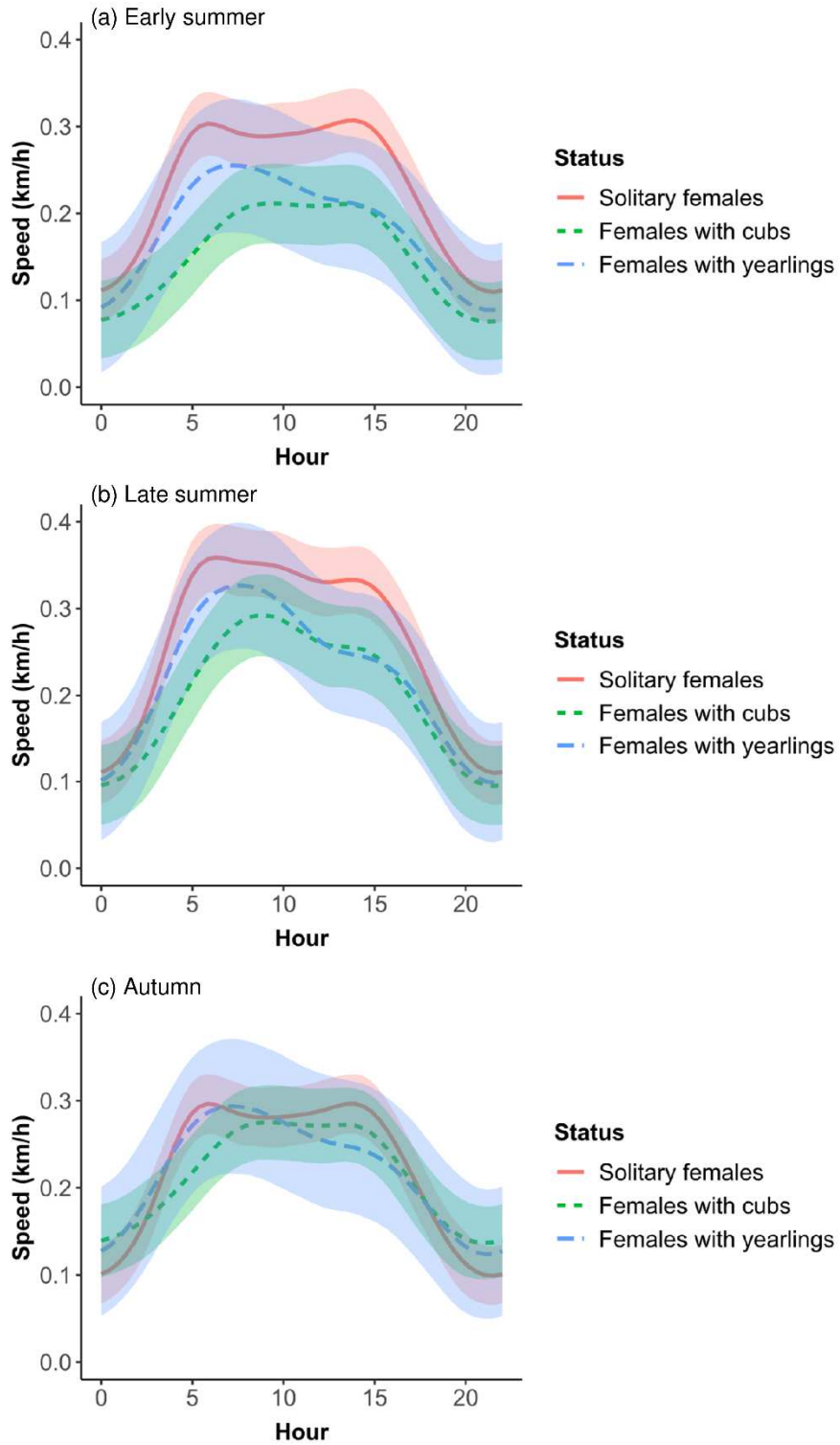


Figure 3-2. Influence of hour on movement velocity in female brown bears on the Shiretoko Peninsula in (a) early summer, (b) late summer, and (c) autumn, as predicted by generalized additive mixed models. Lines indicate model predictions; shading indicates 95% confidence intervals.

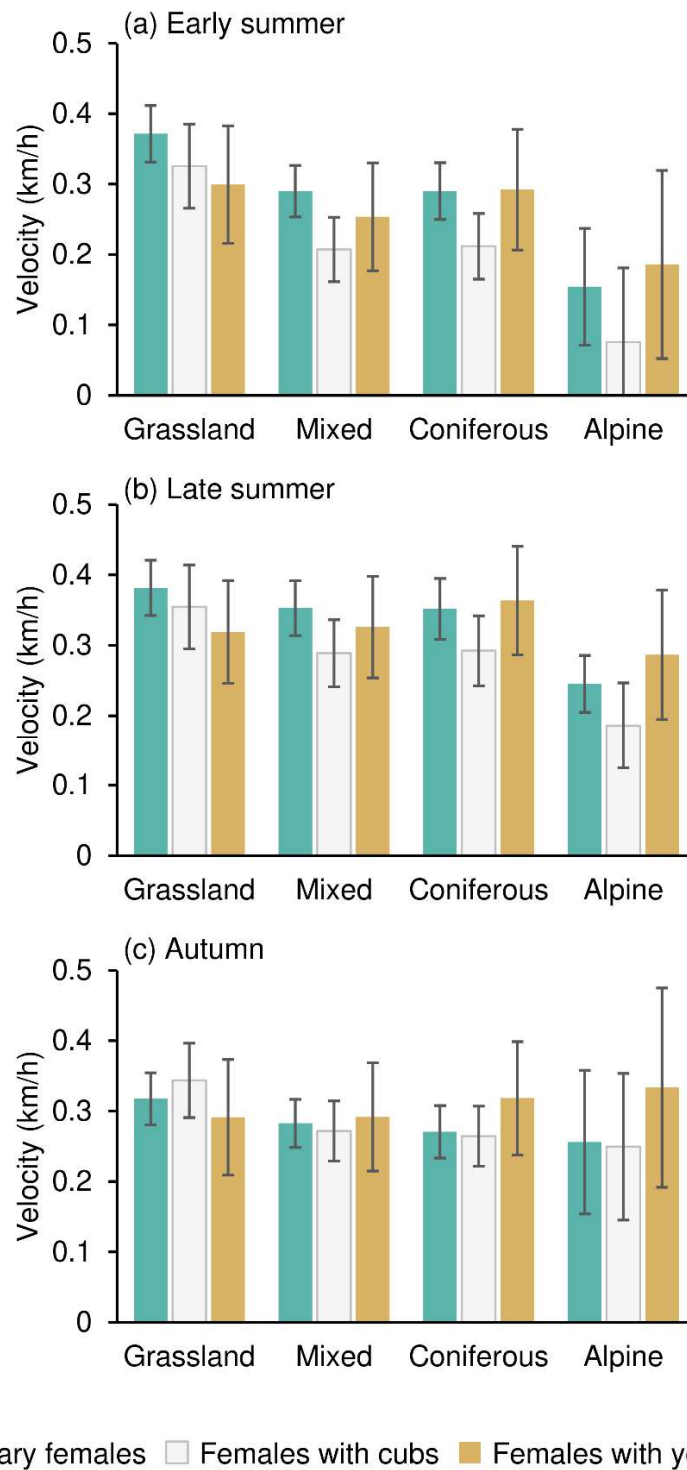


Figure 3-3. Influence of interactions of period, vegetation type, and reproductive status on the hourly speed of female brown bears on the Shiretoko Peninsula, Hokkaido, Japan. (a) Early summer; (b) late summer, and (c) autumn. Bars indicate model predictions; Error bars indicates 95% confidence intervals. “Mixed” denotes deciduous and mixed forest, “Coniferous” denotes coniferous forest, and “Alpine” denotes alpine shrub communities.

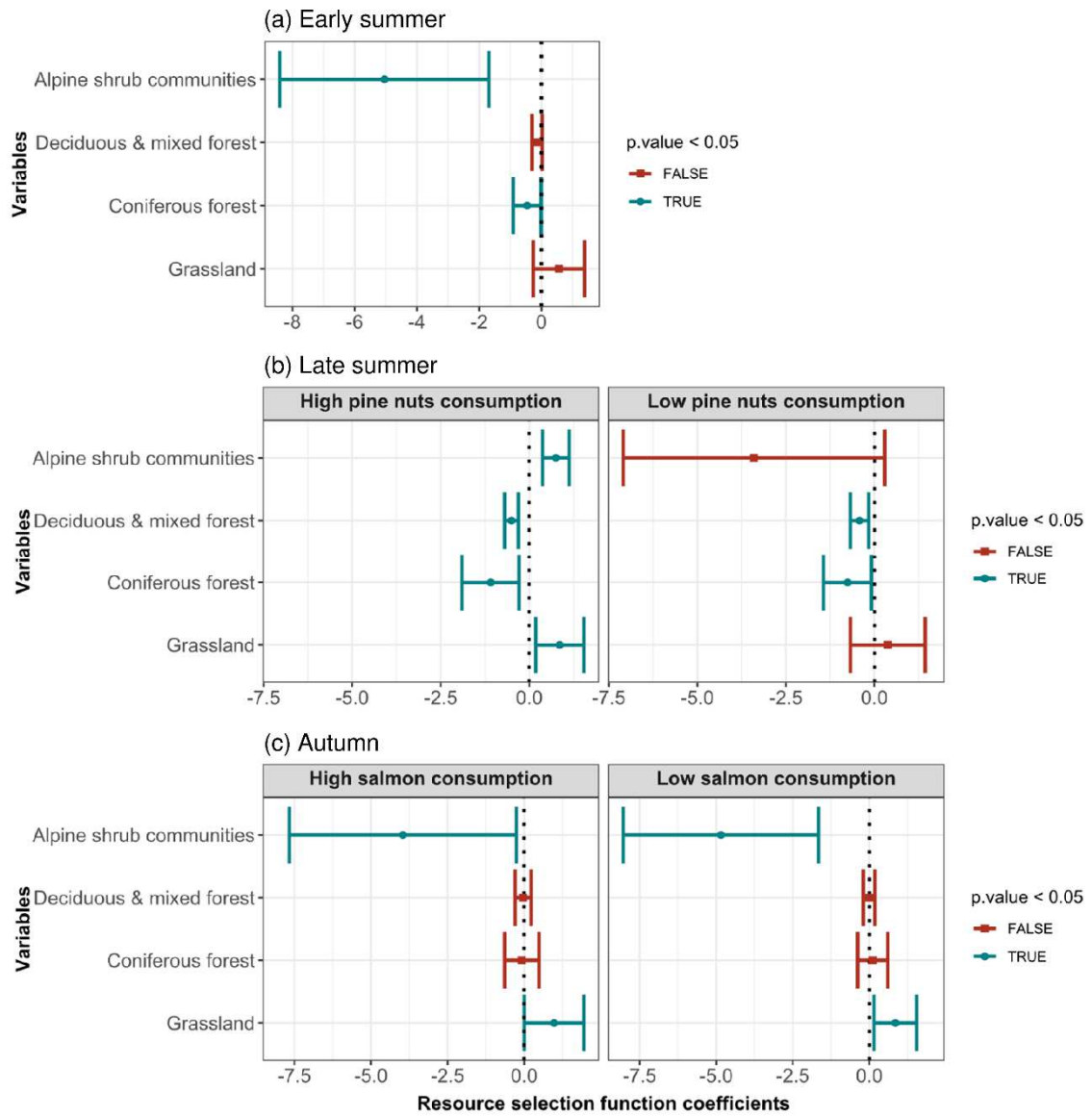


Figure 3-4. Habitat selection coefficients as estimated by resource selection function (RSF) models for brown bears in (a) early summer, (b) late summer, and (c) autumn in the Shiretoko Peninsula, Hokkaido, Japan. Error bars are 95% confidence interval.

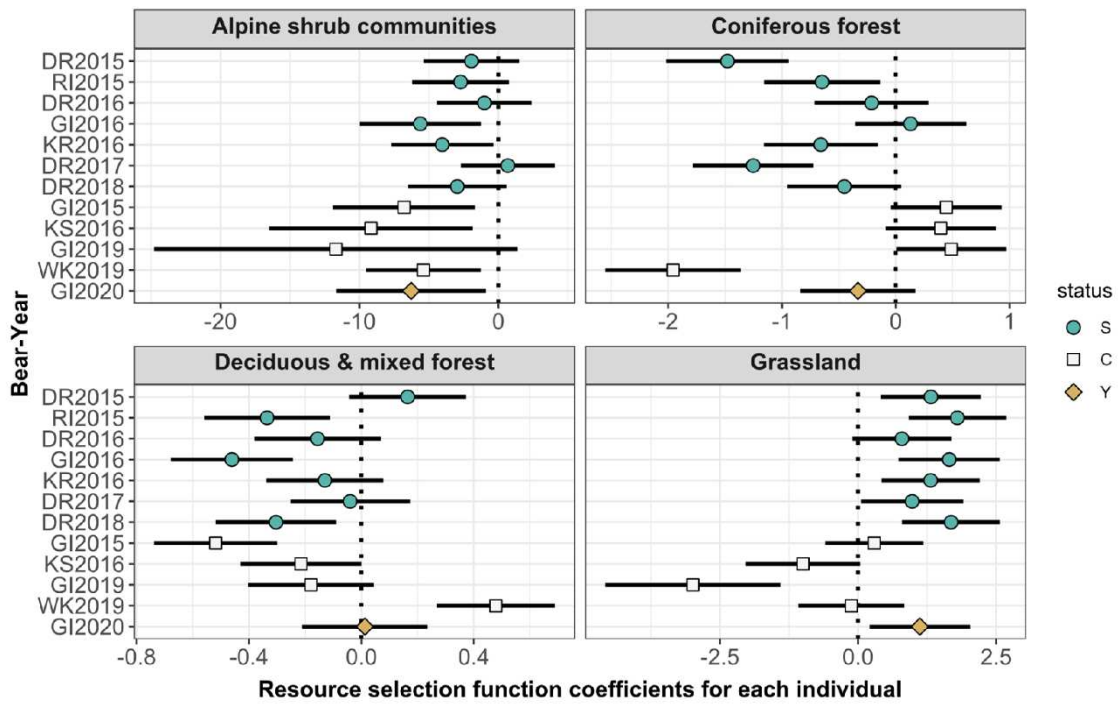


Figure 3-5. Habitat selection coefficients for individuals as estimated by resource selection function (RSF) models for brown bears in early summer in the Shiretoko Peninsula, Hokkaido, Japan. “S” denotes Solitary females, “C” denotes females with cubs, and “Y” denotes females with yearlings. Error bars are 95% confidence interval.

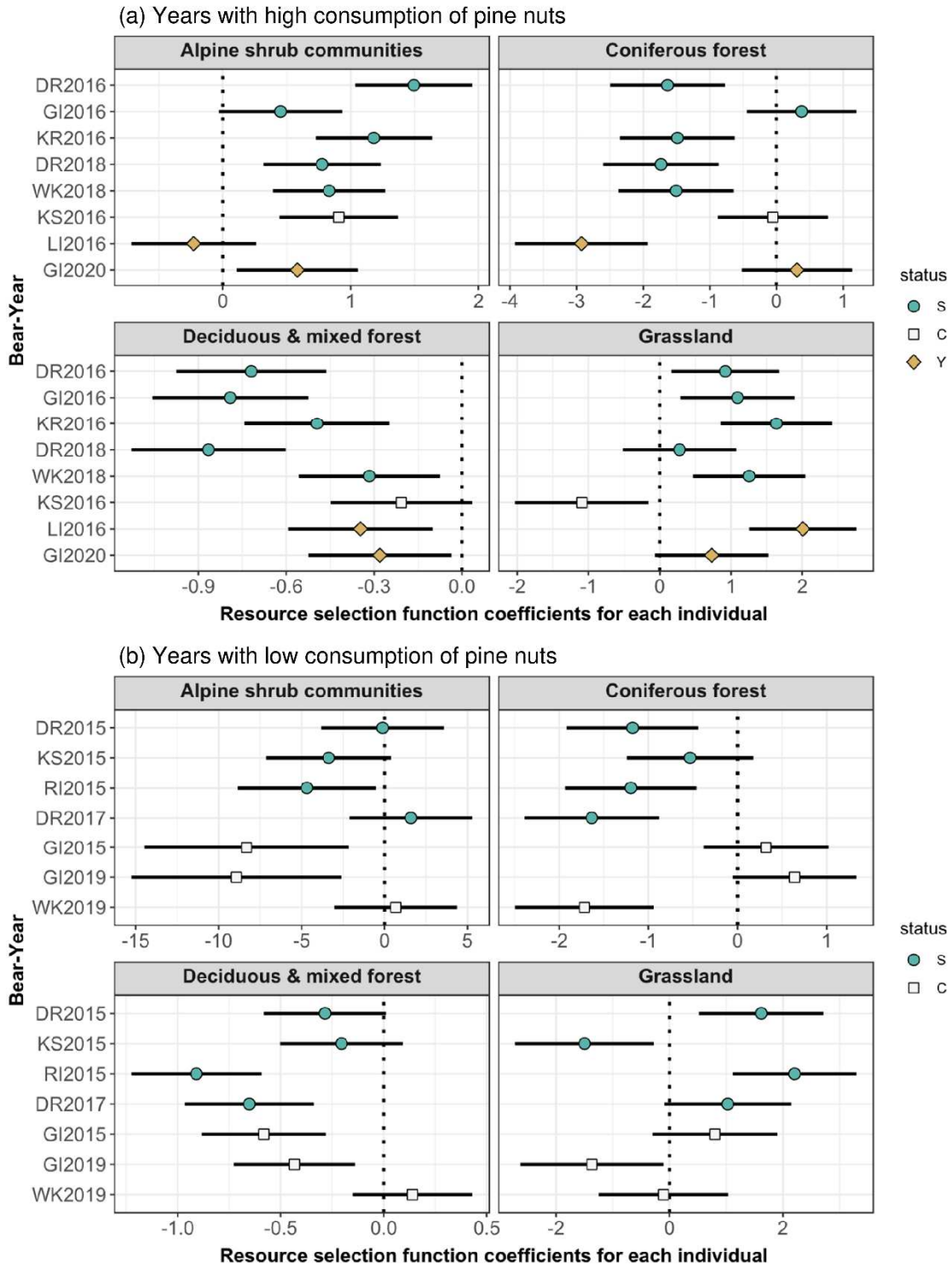


Figure 3-6. Habitat selection coefficients for individuals as estimated by resource selection function (RSF) models for brown bears in late summer, in years with (a) high and (b) low pine nut consumption in the Shiretoko Peninsula, Hokkaido, Japan. “S” denotes Solitary females, “C” denotes females with cubs, and “Y” denotes females with yearlings. Error bars are 95% confidence interval.

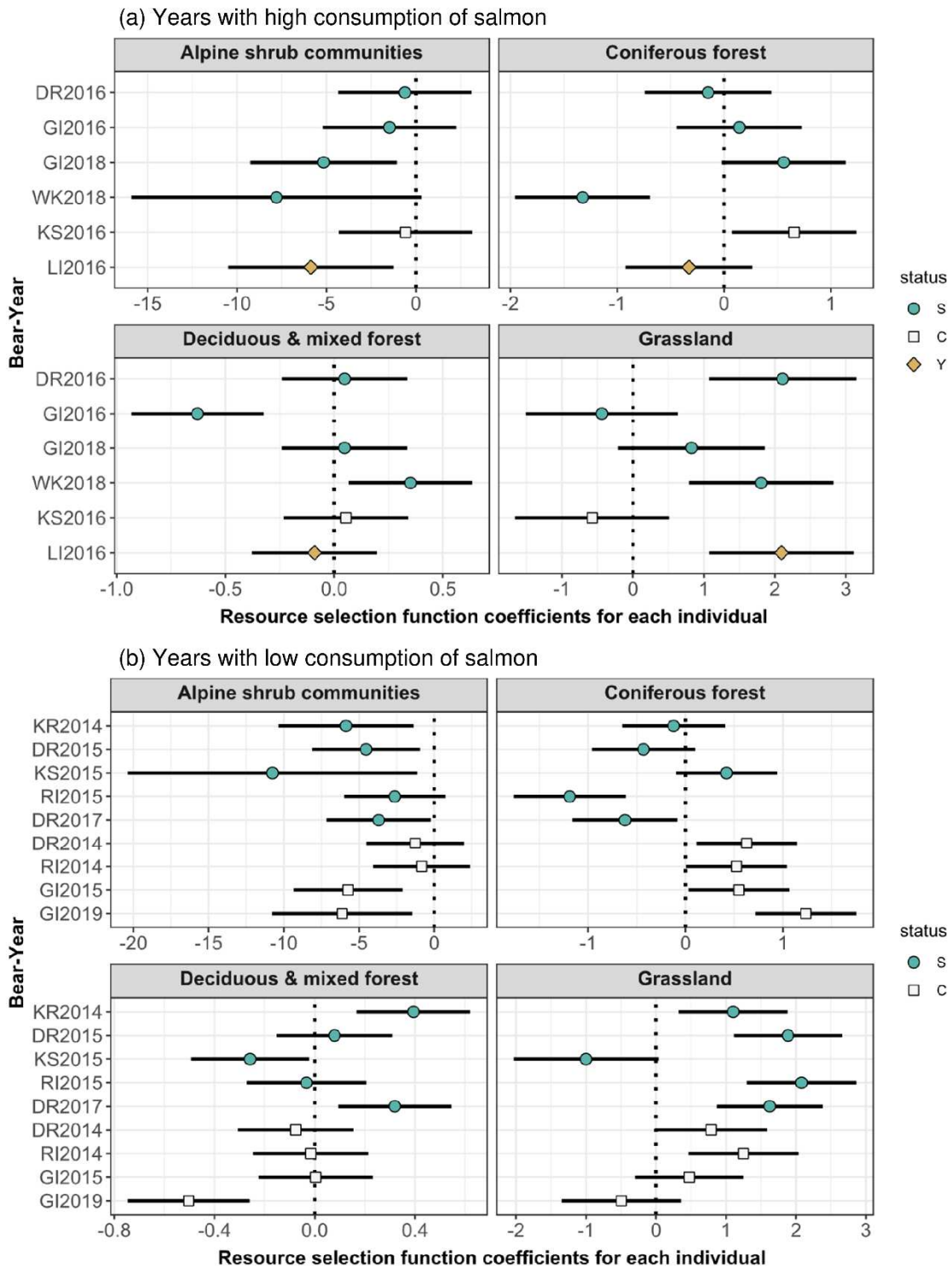


Figure 3-7. Habitat selection coefficients for individuals as estimated by resource selection function (RSF) models for brown bears in autumn, in years with (a) high and (b) low salmon consumption in the Shiretoko Peninsula, Hokkaido, Japan. “S” denotes Solitary females, “C” denotes females with cubs, and “Y” denotes females with yearlings. Error bars are 95% confidence interval.

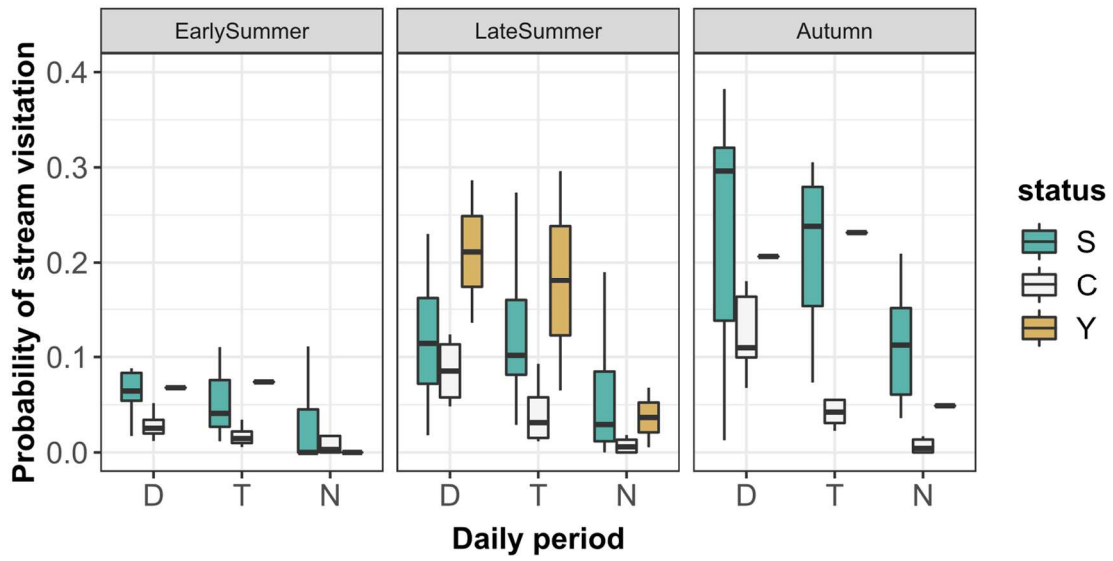


Figure 3-8. Probability of female brown bears visiting salmon spawning sites during one of three time periods for brown bears in the Shiretoko Peninsula, Hokkaido, Japan. Error bars are standard error. “S” denotes Solitary females, “C” denotes females with cubs, and “Y” denotes females with yearlings. “D” denotes daylight, “T” denotes twilight, and “N” denotes nighttime.

SUMMARY

Animal movement is determined by energetic costs associated with acquiring resources. On the Shiretoko Peninsula, Hokkaido, Japan, brown bears frequently travel between the subalpine region and the coastline to forage; however, it remains unknown whether such movement is possible for females with cubs. In this study, we used Global Positioning System location data to clarify changes in female brown bear behavior according to reproductive status and summer diet. This study hypothesized that females with offspring were restricted from obtaining food resources due to the poor mobility of cubs. Hourly movement velocity was calculated by dividing the Euclidean distance between consecutive locations by the associated time lag. In early and late summer, females with cubs moved more slowly compared to solitary females. Vegetation also affected movement velocity, resulting in slow travel in the alpine region. A resource selection function was used to model season-specific habitat selection; bears strongly selected the alpine region only in late summer, regardless of reproductive status. However, in the years with low pine nut consumption, bears avoided the alpine region. This study also found no significant difference in the probability of visiting salmon spawning sites between bears with and without offspring. These findings suggest that female brown bears with cubs are restricted in movement, but do not differ from solitary females in acquiring pine nuts and salmon.

CONCLUSION AND MANAGEMENT IMPLICATION

This study clarified annual variations in the consumption of pine nuts and salmon in late summer and those effects on the body condition and behavior of adult female brown bears in the Shiretoko Peninsula, Hokkaido, Japan. August was the harshest season for brown bears, in particular when bears cannot heavily consume salmon. However, eating a large amount of both pine nuts and salmon enables rapid recovery of body condition of female brown bears. In addition, increased energy expenditure due to cub rearing was probably a great factor leading to poor body condition of females with dependent young. Furthermore, annual fluctuation in pine nuts affected habitat selection of bears in late summer, resulting in bears avoiding alpine regions in years with low pine nut consumption.

These findings may help clarify the cause of the human–bear conflict. Human–bear conflicts, including agricultural crop depredation and intrusion into human residential areas, have become a serious problem in the Shiretoko Peninsula, which often result in the removal of bears as nuisances. Especially in 2012 and 2015, the number of bears killed for nuisance control was nearly twice the usual number, peaking in August. Previous studies on bears have shown that the incidence of human–bear conflicts increases in response to reduced food availability rather than increased population size (Arimoto et al. 2011; Kozakai et al. 2011; Mattson et al. 1992; Su et al. 2018). The present study revealed that the two years with increased human–bear conflict on the Shiretoko Peninsula (2012 and 2015) were consistent with the low consumption of both pine nuts and salmon, suggesting that summer energy shortages may lead to bear intrusion into residential areas. If food shortages trigger the bear intrusion into the residential areas, it can be expected that bears would have poor body conditions due to food shortages in these years. However, the results showed that bears exhibited poor summer body condition not only during 2012 and 2015 but also in other years, indicating that malnutrition is not an indispensable condition for bears to intrude into human settlements. This result is consistent with studies in Japanese black bears (Yamanaka 2011) and Swedish and Slovenian brown bears (Elfström et al. 2014b) that investigated the relationship between the number of bears killed for management and the nutritional status of the killed individuals. Yamanaka (2011) suggested that the feeling of hunger that occurs regardless of the bear’s nutritional status may lead to bear intrusion into residential areas. The low consumption of pine nuts and salmon in the present study may support this theory. On the other

hand, Elfström et al. (2014b) suggested that factors other than food shortages, *i.e.*, avoiding other bears or lack of human experience, explain the bear incidences near settlements. On the Shiretoko Peninsula, maternal human habituation enhances the likelihood of human–bear conflict, especially in young males in the process of dispersal (Shimozuru et al. 2020). Therefore, it is too early to state that food shortages alone cause human–bear conflicts in this brown bear population.

This study has some limitations in understanding the ecology of brown bears throughout the Shiretoko Peninsula. First, this study examined the dynamics of brown bears only in the Rusha area. Due to restricted access and distance from the residential areas, bears in this area may behave differently than bears living near the human settlements (Shimozuru et al. 2020). In addition, because there are probably differences in access to food resources within the Shiretoko Peninsula (Matsubayashi et al. 2014), it may be difficult to determine the cause of human–bear conflict based solely on the food habits of bears in the Rusha area. Conversely, the fact that this study was able to clarify the diet and behavior of brown bears far from the residential area is also a great advantage. In future research, I hope to clarify the characteristics of bears that appear in the human settlements by comparing the food habits and behavior of brown bears around the residential areas with the results of this study. Second, this study examined the ecology of adult females only. Previous studies in Sweden have shown that there is no difference in the body condition and its seasonal pattern between problem bears (*i.e.*, bears killed by managers) and nonproblem bears (*i.e.*, bears killed by hunters), and that the frequency of artificial food use varies with sex-age class rather than nutritional status (Elfström et al. 2014a, 2014b). To better understand the mechanisms of bear intrusion, further studies investigating individual differences in diet and in consumption of high-nutrition foods are required.

The conservation and management of large mammals is a difficult task that requires not only scientific knowledge, but also social, political, and economic circumstances. The Shiretoko Peninsula, with its wildlife protection areas, farmlands, fishermen's settlements, residential areas, and also tourist spots, can be a good model area for thoroughly investigating the complex relationships between wildlife and humans. The unique dataset of individual-based long-term monitoring data for Shiretoko brown bears allowed this study to disentangle the relationship between diet, nutritional status, and behavior of brown bears. I hope that empirical research on the Shiretoko Peninsula will continue for a long time, and that it will clarify the effects of maternal learning, personality, and human habituation on the energy balance and behavior of brown bears. Such research should give us hints on how to build better relationships with wildlife.

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DEDICATION

This work is dedicated to the brown bears on the Shiretoko Peninsula. Without their tolerance and cooperation this project would never have been possible.

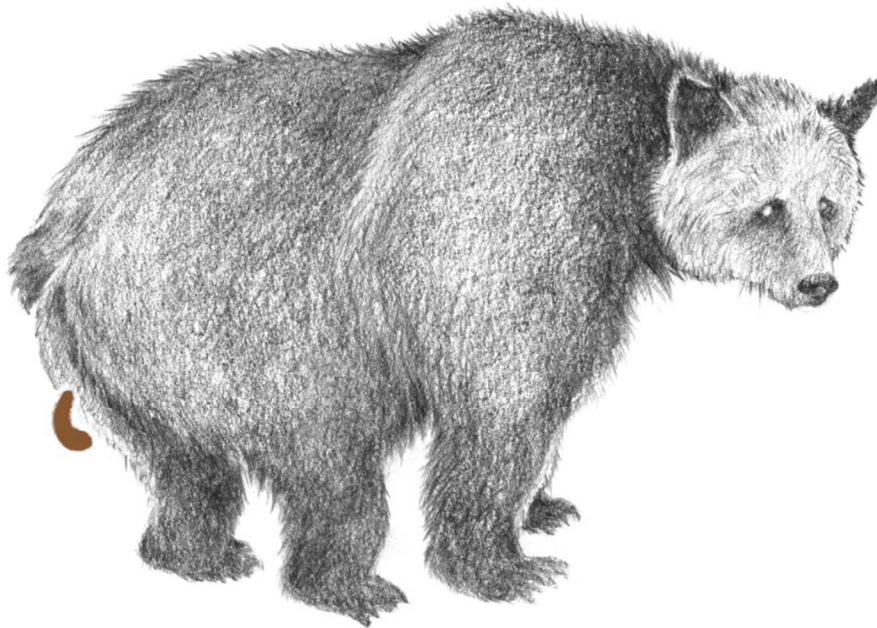


Illustration by T. Shirane

BIBLIOGRAPHY

- Amstrup SC, Stirling I, and Lentfer JW. 1986. Past and present status of polar bears in Alaska. *Wildlife Society Bulletin* 14(3): 241–254.
- Aoi T. 1985. Seasonal change in food habits of Ezo brown bear (*Ursus arctos yesoensis* Lydekker) in Northern Hokkaido. *Research Bulleteins of the College Experiment Forests Hokkaido University* 42(4): 721–732.
- Arimoto I, Goto Y, Nagai C, and Furubayashi K. 2011. Autumn food habits and home-range elevations of Japanese black bears in relation to hard mast production in the beech family in Toyama Prefecture. *Mammal Study* 36(4): 199–208.
- Atkinson SN, Nelson RA, and Ramsay MA. 1996. Changes in the body composition of fasting polar bears (*Ursus maritimus*): The effect of relative fatness on protein conservation. *Physiological Zoology* 69(2): 304–316.
- Atkinson SN, and Ramsay MA. 1995. The effects of prolonged fasting of the body composition and reproductive success of female Polar Bears (*Ursus maritimus*). *Functional Ecology* 9(4): 559–567.
- Bartareau TM. 2017. Estimating the live body weight of American black bears in Florida. *Journal of Fish and Wildlife Management* 8(1): 234–239.
- Bartareau TM, Cluff HD, and Larter NC. 2011. Body length and mass growth of the brown bear (*Ursus arctos*) in northern Canada: Model selection based on information theory and ontogeny of sexual size dimorphism. *Canadian Journal of Zoology* 89(11): 1128–1135.
- Bartoń K. 2020. Mu-MIn : Multi-model inference. R package version 1.43.17. <https://cran.r-project.org/package=MuMIn> (accessed 14 October 2020).
- Baruch-Mordo S, Wilson KR, Lewis DL, Broderick J, Mao JS, and Breck SW. 2014. Stochasticity in Natural Forage Production Affects Use of Urban Areas by Black Bears: Implications to Management of Human-Bear Conflicts. *PLoS ONE* 9(1): e85122.
- Bates D, Mächler M, Bolker BM, and Walker SC. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1): 1–48.
- Baty F, Ritz C, Charles S, Brutsche M, Flandrois J-P, and Delignette-Muller M-L. 2015. A toolbox for nonlinear regression in R: The package nlstools. *Journal of Statistical Software* 66(5): 1–21.
- Bellemain E, Swenson JE, and Taberlet P. 2006. Mating strategies in relation to sexually

BIBLIOGRAPHY

- selected infanticide in a non-social carnivore: the brown bear. *Ethology* 112(3): 238–246.
- Ben-David M, Titus K, and Beier LVR. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138(3): 465–474.
- Blanchard BM. 1987. Size and growth patterns of the Yellowstone grizzly bear. *Bears: Their Biology and Management* 7: 99–107.
- Blanchard BM, and Knight RR. 1991. Movements of yellowstone grizzly bears. *Biological Conservation* 58(1): 41–67.
- Bojarska K, and Selva N. 2013. Correction factors for important brown bear foods in Europe. *Ursus* 24(1): 13–15.
- Bojarska K, and Selva N. 2012. Spatial patterns in brown bear *Ursus arctos* diet: The role of geographical and environmental factors. *Mammal Review* 42(2): 120–143.
- Boswell T, Woods SC, and Kenagy GJ. 1994. Seasonal changes in body mass, insulin, and glucocorticoids of free-living golden-mantled ground squirrels. *General and Comparative Endocrinology* 96(3): 339–346.
- Brown JH, Gilgooly JF, Allen AP, Savage VM, and West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85(7): 1771–1789.
- Burkholder WJ. 2000. Use of body condition scores in clinical assessment of the provision of optimal nutrition. *Journal of the American Veterinary Medical Association* 217(5): 650–654.
- Burnham KP, and Anderson DR. 2002. Model selection and multimodel inference - A practical information-Theoretic approach, Second. ed. Springer-Verlag, New York, U.S.A.
- Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197(3–4): 516–519.
- Cattet MRL. 2000. Biochemical and physiological aspects of obesity, high fat diet, and prolonged fasting in free-ranging polar bears. Ph.D. Thesis, University of Saskatchewan, Saskatoon, Canada.
- Cattet MRL. 1990. Predicting nutritional condition in black bears and polar bears on the basis of morphological and physiological measurements. *Canadian Journal of Zoology* 68(1): 32–39.
- Cattet MRL, Caulkett NA, Obbard ME, and Stenhouse GB. 2002. A body-condition index for ursids. *Canadian Journal of Zoology* 80(7): 1156–1161.
- Cattet MRL, and Obbard ME. 2005. To weigh or not to weigh: conditions for the estimation of body mass by morphometry. *Ursus* 16(1): 102–107.
- Christiansen F, Vivier F, Charlton C, Ward R, Amerson A, Burnell S, and Bejder L. 2018.

BIBLIOGRAPHY

- Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series* 592: 267–281.
- Ciarniello LM, Boyce MS, Heard DC, and Seip DR. 2005. Denning behavior and den site selection of grizzly bears along the Parsnip River, British Columbia, Canada. *Ursus* 16(1): 47–58.
- Cicnjak L, Huber D, Roth HU, Ruff RL, and Vinovrski Z. 1987. Food habits of brown bears in Plitvice Lakes National Park, Yugoslavia. *Bears: Their Biology and Management* 7: 221–226.
- Ciucci P, Tosoni E, Di Domenico G, Quattrociochi F, and Boitani L. 2014. Seasonal and annual variation in the food habits of Apennine brown bears, central Italy. *Journal of Mammalogy* 95(3): 572–586.
- Clapham M, Miller E, Nguyen M, and Darimont CT. 2020. Automated facial recognition for wildlife that lack unique markings: A deep learning approach for brown bears. *Ecology and Evolution* 10(23): 12883–12892.
- Clapham M, Nevin OT, Ramsey AD, and Rosell F. 2014. Scent-marking investment and motor patterns are affected by the age and sex of wild brown bears. *Animal Behaviour* 94: 107–116.
- Clapham M, Nevin OT, Ramsey AD, and Rosell F. 2012. A Hypothetico-deductive approach to assessing the social function of chemical signalling in a non-territorial solitary carnivore. *PLoS ONE* 7(4): e35404.
- Clutton-Brock T, and Sheldon BC. 2010. Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution* 25(10): 562–573.
- Cook JG, Johnson BK, Cook RC, Riggs RA, Delcurto T, Bryant LD, and Irwin LL. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155(1): 1–61.
- Costello CM, Creel SR, Kalinowski ST, Vu N V., and Quigley HB. 2008. Sex-biased natal dispersal and inbreeding avoidance in American black bears as revealed by spatial genetic analyses. *Molecular Ecology* 17(21): 4713–4723.
- Costello CM, van Manen FT, Haroldson MA, Ebinger MR, Cain SL, Gunther KA, and Bjornlie DD. 2014. Influence of whitebark pine decline on fall habitat use and movements of grizzly bears in the Greater Yellowstone Ecosystem. *Ecology and Evolution* 4(10): 2004–2018.
- Craighead JJ, Sumner JS, and Mitchell JA. 1995. The grizzly bears of Yellowstone : their ecology in the Yellowstone ecosystem, 1959-1992. Island Press, Washington DC, U.S.A.

BIBLIOGRAPHY

- Dahle B, Sørensen OJ, Wedul EH, Swenson JE, and Sandegren F. 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. *Wildlife Biology* 4(2): 147–158.
- Dahle B, and Swenson JE. 2003a. Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. *Behavioral Ecology and Sociobiology* 54(4): 352–358.
- Dahle B, and Swenson JE. 2003b. Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology* 72: 660–667.
- Deacy W, Leacock W, Armstrong JB, and Stanford JA. 2016. Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. *Ecology* 97(5): 1091–1098.
- Delibes M, Gaona P, and Ferreras P. 2001. Effects of an attractive sink leading into maladaptive habitat selection. *The American Naturalist* 158(3): 277–285.
- Department for Environment Food and Rural Affairs. 2004. Pigs: Condition Scoring (PB3480) - How to Condition Score. <http://adlib.everysite.co.uk/adlib/defra/content.aspx?id=000IL3890W.185EBLT3WHE457> (accessed 11 August 2020).
- Derocher AE, Andersen M, Wiig Ø, Aars J, Hansen E, and Biuw M. 2011. Sea ice and polar bear den ecology at Hopen Island, Svalbard. *Marine Ecology Progress Series* 441: 273–279.
- Derocher AE, and Stirling I. 1998. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). *Journal of Zoology* 245(3): 253–260.
- Derocher AE, and Wiig Ø. 2002. Postnatal growth in body length and mass of polar bears (*Ursus maritimus*) at Svalbard. *Journal of Zoology* 256(3): 343–349.
- Eagle TC, and Pelton MR. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. *International Conference on Bear Research and Management* 5: 94–101.
- Elfström M, Davey ML, Zedrosser A, Müller M, De Barba M, Støen OG, Miquel C, Taberlet P, Hackländer K, and Swenson JE. 2014a. Do Scandinavian brown bears approach settlements to obtain high-quality food? *Biological Conservation* 178: 128–135.
- Elfström M, Zedrosser A, Jerina K, Støen O, Kindberg J, Budic L, Jonozovič M, and Swenson JE. 2014b. Does despotic behavior or food search explain the occurrence of problem brown bears in Europe? *The Journal of Wildlife Management* 78(5): 881–893.
- Fandos Esteruelas N, Cattet MRL, Zedrosser A, Stenhouse GB, Küker S, Evans AL, and Arnemo JM. 2017. A Double-Blinded, Randomized Comparison of Medetomidine-

BIBLIOGRAPHY

- Tiletamine-Zolazepam and Dexmedetomidine-Tiletamine-Zolazepam Anesthesia in Free-Ranging Brown Bears (*Ursus arctos*). *PLOS ONE* 12(1): e0170764.
- Farley SD, and Robbins CT. 1994. Development of two methods to estimate body composition of bears. *Canadian Journal of Zoology* 72(2): 220–226.
- Felicetti LA, Robbins CT, and Shipley LA. 2003. Dietary protein content alters energy expenditure and composition of the mass gain in grizzly bears (*Ursus arctos horribilis*). *Physiological and Biochemical Zoology* 76(2): 256–261.
- Feltz CJ, and Miller GE. 1996. An asymptotic test for the equality of coefficients of variation from k populations. *Statistics in medicine* 15(6): 647–658.
- Fietz J, and Ganzhorn JU. 1999. Feeding ecology of the hibernating primate *Cheirogaleus medius*: How does it get so fat? *Oecologia* 121(2): 157–164.
- Frąckowiak W, Theuerkauf J, Pirga B, and Gula R. 2014. Brown bear habitat selection in relation to anthropogenic structures in the Bieszczady Mountains, Poland. *Biologia* 69(7): 926–930.
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, and Toïgo C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31(1): 367–393.
- Gardner CL, Pamperin NJ, and Benson JF. 2014. Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska. *Ursus* 25(2): 121–138.
- Gau RJ, and Case R. 1999. Evaluating nutritional condition of grizzly bears via select blood parameters. *The Journal of Wildlife Management* 63(1): 286–291.
- Gosler AG. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *The Journal of Animal Ecology* 65: 1–17.
- Goszczyński J, Jedrzejewska B, and Jedrzejewski W. 2000. Diet composition of badgers (*Meles meles*) in a pristine forest and rural habitats of Poland compared to other European populations. *Journal of Zoology* 250(4): 495–505.
- Guinet C, Roux JP, Bonnet M, and Mison V. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology* 76(8): 1418–1424.
- Gunther KA, Haroldson MA, Frey K, Cain SL, Copeland J, and Schwartz CC. 2004. Grizzly bear-human conflicts in the Greater Yellowstone ecosystem, 1992-2000. *Ursus* 15(1): 10–22.
- Helldin J-O. 1999. Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography* 22(3): 324–336.
- Hellgren EC, Rogers LL, and Seal US. 1993. Serum chemistry and hematology of black bears:

BIBLIOGRAPHY

- physiological indices of habitat quality or seasonal patterns? *Journal of Mammalogy* 74(2): 304–315.
- Hellgren EC, Vaughan MR, and Kirkpatrick RL. 1989. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia-North Carolina. *Canadian Journal of Zoology* 67(8): 1837–1850.
- Henneke DR, Potter GD, Kreider JL, and Yeates BF. 1983. Relationship between condition score, physical measurements and body fat percentage in mares. *Equine Veterinary Journal* 15(4): 371–372.
- Hertel AG, Bischof R, Langval O, Mysterud A, Kindberg J, Swenson JE, and Zedrosser A. 2018. Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos* 127(2): 197–207.
- Hertel AG, Zedrosser A, Kindberg J, Langvall O, and Swenson JE. 2019. Fluctuating mast production does not drive Scandinavian brown bear behavior. *The Journal of Wildlife Management* 83(3): 657–668.
- Hewitt DG, and Robbins CT. 1996. Estimating grizzly bear food habits from fecal analysis. *Wildlife Society Bulletin* 24(3): 547–550.
- Hilderbrand G V., Farley SD, and Robbins CT. 1998. Predicting body condition of bears via two field methods. *The Journal of Wildlife Management* 62(1): 406–409.
- Hilderbrand G V., Gustine DD, Mangipane BA, Joly K, Leacock W, Mangipane LS, Erlenbach J, Sorum MS, Cameron MD, Belant JL, and Cambier T. 2018. Body size and lean mass of brown bears across and within four diverse ecosystems. *Journal of Zoology* 305(1): 53–62.
- Hilderbrand G V., Jenkins SG, Schwartz CC, Hanley TA, and Robbins CT. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology* 77(10): 1623–1630.
- Hilderbrand G V., Schwartz CC, Robbins CT, and Hanley TA. 2000. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. *The Journal of Wildlife Management* 64(1): 178–183.
- Hilderbrand G V., Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, and Servheen C. 1999b. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77(1): 132–138.
- Hokkaido Government. 2017. Brown bear management plan in Hokkaido (in Japanese). http://www.pref.hokkaido.lg.jp/ks/skn/higuma/hokkaido_bear_management_plan05.pdf (accessed 8 July 2017).
- Horikawa M, Tsuyama I, Matsui T, Kominami Y, and Tanaka N. 2009. Assessing the potential

BIBLIOGRAPHY

- impacts of climate change on the alpine habitat suitability of Japanese stone pine (*Pinus pumila*). *Landscape Ecology* 24(1): 115–128.
- Hrdy SB. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1(1): 13–40.
- Joblon MJ, Pokras MA, Morse BJ, Harry CT, Rose KS, Sharp SM, Niemeyer ME, Patchett K, Sharp WB, and Moore MJ. 2015. Body condition scoring system for delphinids based on short-beaked common dolphins (*Delphinus delphis*). *Journal of Marine Animals and Their Ecology* 7(2): 5–13.
- Johnson DH. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61(1): 65–71.
- Johnson HE, Breck SW, Baruch-Mordo S, Lewis DL, Lackey CW, Wilson KR, Broderick J, Mao JS, and Beckmann JP. 2015. Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States. *Biological Conservation* 187: 164–172.
- Judd SL, Knight RR, and Blanchard BM. 1986. Denning of grizzly bears in the Yellowstone National Park area. *Bears: Their Biology and Management* 6: 111–117.
- Kaczensky P, Huber D, Knauer F, Roth H, Wagner A, and Kusak J. 2006. Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *Journal of Zoology* 269(4): 474–485.
- Kaeriyama M. 2008. Ecosystem-based sustainable conservation and management of Pacific salmon, in: Tsukamoto, K., Kawamura, T., Takeuchi, T., Beard, T. Douglas, J., Kaiser, M.J. (Eds.), *Fisheries for Global Welfare and Environment, Memorial Book of the 5th World Fisheries Congress 2008*. TERRAPUB, Tokyo, pp. 371–380.
- Kasbohm JW, Vaughan MR, and Kraus JG. 1998. Black bear home range dynamics and movement patterns during a Gypsy Moth Infestation. *Ursus* 10: 259–267.
- Kavčič I, Adamič M, Kaczensky P, Krofel M, Kobal M, and Jerina K. 2015. Fast food bears: brown bear diet in a human-dominated landscape with intensive supplemental feeding. *Wildlife Biology* 21(1): 1–8.
- Kingsley MCS, Nagy JA, and Reynolds H V. 1988. Growth in length and weight of northern brown bears: differences between sexes and populations. *Canadian Journal of Zoology* 66(4): 981–986.
- Kishi M, Kaeriyama M, Ueno H, and Kamezawa Y. 2010. The effect of climate change on the growth of Japanese chum salmon (*Oncorhynchus keta*) using a bioenergetics model coupled with a three-dimensional lower trophic ecosystem model (NEMURO). *Deep-Sea Research Part 2. Topical Studies in Oceanography* 57(13–14): 1257–1265.

BIBLIOGRAPHY

- Klinka DR, and Reimchen TE. 2009. Darkness, twilight, and daylight foraging success of bears (*Ursus americanus*) on salmon in coastal British Columbia. *Journal of Mammalogy* 90(1): 144–149.
- Kohira M, Okada H, Nakanishi M, and Yamanaka M. 2009. Modeling the effects of human-caused mortality on the brown bear population on the Shiretoko Peninsula, Hokkaido, Japan. *Ursus* 20: 12–21.
- Koike S, Kozakai C, Nemoto Y, Masaki T, Yamazaki K, Abe S, Nakajima A, Umemura Y, and Kaji K. 2012. Effect of hard mast production on foraging and sex-specific behavior of the Asiatic black bear (*Ursus thibetanus*). *Mammal Study* 37(1): 21–28.
- Kozakai C, Yamazaki K, Nemoto Y, Nakajima A, Koike S, Abe S, Masaki T, and Kaji K. 2011. Effect of mast production on home range use of Japanese black bears. *The Journal of Wildlife Management* 75(4): 867–875.
- Labocha MK, Schutz H, and Hayes JP. 2014. Which body condition index is best? *Oikos* 123(1): 111–119.
- Laflamme DP. 2012. Companion animals symposium: obesity in dogs and cats: what is wrong with being fat? *Journal of Animal Science* 90(5): 1653–1662.
- Lamb CT, Mowat G, McLellan BN, Nielsen SE, and Boutin S. 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology* 86(1): 55–65.
- Lenth R. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.0. <https://cran.r-project.org/package=emmeans> (accessed 24 June 2020).
- López-Alfaro C, Coogan SCP, Robbins CT, Fortin JK, and Nielsen SE. 2015. Assessing nutritional parameters of brown bear diets among ecosystems gives insight into differences among populations. *PLOS ONE* 10(6): e0128088.
- Macfarlane WW, Logan JA, and Kern WR. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. *Ecological Applications* 23(2): 421–437.
- Mahoney SP, Virgl JA, and Mawhinney K. 2001. Potential mechanisms of phenotypic divergence in body size between Newfoundland and mainland black bear populations. *Canadian Journal of Zoology* 79(9): 1650–1660.
- Makino M, and Sakurai Y. 2012. Adaptation to climate-change effects on fisheries in the Shiretoko World Natural Heritage area, Japan. *ICES Journal of Marine Science* 69(7): 1134–1140.
- Manly BFJ, Miller P, and Cook LM. 1972. Analysis of a selective predation experiment. *The American Naturalist* 106(952): 719–736.

BIBLIOGRAPHY

- Mano T, and Tsubota T. 2002. Reproductive characteristics of brown bears on the Oshima Peninsula, Hokkaido, Japan. *Journal of Mammalogy* 83(4): 1026–1034.
- Martin J, van Moorter B, Revilla E, Blanchard P, Dray S, Quenette P-Y, Allainé D, and Swenson JE. 2013. Reciprocal modulation of internal and external factors determines individual movements. *Journal of Animal Ecology* 82(2): 290–300.
- Marzluff JM, Millsbaugh JJ, Hurvitz P, and Handcock MS. 2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller's Jays. *Ecology* 85(5): 1411–1427.
- Matsubayashi J, Morimoto J, Mano T, Aryal A, and Nakamura F. 2014. Using stable isotopes to understand the feeding ecology of the Hokkaido brown bear (*Ursus arctos*) in Japan. *Ursus* 25(2): 87–97.
- Mattson DJ, Barber K, Maw R, and Renkin R. 2004. Coefficients of productivity for Yellowstone's grizzly bear habitat, Biological Science Report 2002-0007. U.S. Fish and Wildlife Service, Corvallis, Oregon, U.S.A.
- Mattson DJ, Blanchard BM, and Knight RR. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *The Journal of Wildlife Management* 56(3): 432–442.
- Mattson DJ, Blanchard BM, and Knight RR. 1991. Food habits of Yellowstone grizzly bears, 1977-1987. *Canadian Journal of Zoology* 69(6): 1619–1629.
- McClelland CJR, Coops NC, Kearney SP, Burton AC, Nielsen SE, and Stenhouse GB. 2020. Variations in grizzly bear habitat selection in relation to the daily and seasonal availability of annual plant-food resources. *Ecological Informatics* 58: 101116.
- McLellan BN. 2015. Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *The Journal of Wildlife Management* 79(5): 749–765.
- McLellan BN. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. *Canadian Journal of Zoology* 89(6): 546–558.
- McLellan BN. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16(2): 141–156.
- McLellan BN. 1994. Density-dependent population regulation of brown bears, in: Taylor, M. (Ed.), Int. Conf. Bear Res. and Manage. Monogr. Series No. 3. International Association for Bear Research and Management, Missoula, Montana, U.S.A., pp. 15–24.
- McLellan BN, and Hovey FW. 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. *Canadian Journal of Zoology* 73(4): 704–712.
- Mealey SP. 1980. The Natural food habits of grizzly bears in Yellowstone National Park, 1973-

BIBLIOGRAPHY

74. *Bears: Their Biology and Management* 4: 281–292.
- Microsoft Corporation. 2016. Microsoft Excel. <https://office.microsoft.com/excel> (accessed 20 September 2016).
- Miller SD, Sellers RA, and Keay JA. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* 14(2): 130–152.
- Moe TF, Kindberg J, Jansson I, and Swenson JE. 2007. Importance of diel behaviour when studying habitat selection: Examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology* 85(4): 518–525.
- Morfeld KA, Lehnhardt J, Alligood C, Bolling J, and Brown JL. 2014. Development of a body condition scoring index for female African elephants validated by ultrasound measurements of subcutaneous fat. *PLOS ONE* 9(4): e93802.
- Moriwaki J, Omori R, Shimozuru M, Tsuruga H, Mano T, and Tsubota T. 2018. Evaluation of body condition using body mass and chest girth in brown bears of Hokkaido, Japan (*Ursus arctos yesoensis*). *Japanese Journal of Veterinary Research* 66(2): 71–81.
- Mowat G, and Heard DC. 2006. Major components of grizzly bear diet across North America. *Canadian Journal of Zoology* 84(3): 473–489.
- Munro RHM, Nielsen SE, Price MH, Stenhouse GB, and Boyce MS. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87(6): 1112–1121.
- Nakamura F, and Komiyama E. 2010. A challenge to dam improvement for the protection of both salmon and human livelihood in Shiretoko, Japan's third Natural Heritage Site. *Landscape and Ecological Engineering* 6(1): 143–152.
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, and Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105(49): 19052–19059.
- Nelson RA, Folk GE, Pfeiffer EW, Craighead JJ, Jonkel CJ, and Steiger DL. 1983. Behavior, Biochemistry, and Hibernation in Black, Grizzly, and Polar Bears. *Bears: Their Biology and Management* 5: 284–290.
- Niedziałkowska M, Hayward MW, Borowik T, Jędrzejewski W, and Jędrzejewska B. 2019. A meta-analysis of ungulate predation and prey selection by the brown bear *Ursus arctos* in Eurasia. *Mammal Research* 64(1): 1–9.
- Nielsen SE, Stenhouse GB, and Boyce MS. 2006. A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation* 130(2): 217–229.
- Noonan MJ, Markham A, Newman C, Trigoni N, Buesching CD, Ellwood SA, and Macdonald DW. 2014. Climate and the individual: Inter-annual variation in the autumnal activity of

BIBLIOGRAPHY

- the European badger (*Meles meles*). *PLOS ONE* 9(1): e83156.
- Noyce K V, and Garshelis DL. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. *Bears: Their Biology and Management* 9(1): 481–496.
- Ogle DH, Wheeler P, and Dinno A. 2020. FSA: Fisheries Stock Analysis. R package version 0.8.30. <https://github.com/droglenc/FSA> (accessed 7 May 2020).
- Ohdachi S, and Aoi T. 1987. Food habits of brown bears in Hokkaido, Japan. *Bears: Their Biology and Management* 7: 215–220.
- Olson TL, Squibb RC, and Gilbert BK. 1998. Brown bear diurnal activity and human use: a comparison of two salmon streams. *Ursus* 10: 547–555.
- Ordiz A, Rodríguez C, Naves J, Fernández A, Huber D, Kaczensky P, Mertens A, Mertzanis Y, Mustoni A, Palazón S, Quenette PY, Rauer G, and Swenson JE. 2007. Distance-based criteria to identify minimum number of brown bear females with cubs in Europe. *Ursus* 18(2): 158–167.
- Otto KL, Ferguson JD, Fox DG, and Sniffen CJ. 1991. Relationship between body condition score and composition of ninth to eleventh rib tissue in Holstein dairy cows. *Journal of Dairy Science* 74(3): 852–859.
- Parker KL, Barboza PS, and Gillingham MP. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23(1): 57–69.
- Peig J, and Green AJ. 2009. New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos* 118(12): 1883–1891.
- Penteriani V, Delgado MDM, Krofel M, Jerina K, Ordiz A, Dalerum F, Zarzo-Arias A, and Bombieri G. 2018. Evolutionary and ecological traps for brown bears *Ursus arctos* in human-modified landscapes. *Mammal Review* 48(3): 180–193.
- Penteriani V, Zarzo-Arias A, del Mar Delgado M, Dalerum F, Gurarie E, Torre PP, Corominas TS, Vázquez VM, García PV, and Ordiz A. 2020. Female brown bears use areas with infanticide risk in a spatially confined population. *Ursus* 2020(31e2): 1.
- Perryman WL, and Lynn MS. 2002. Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *Journal of Cetacean Research and Management* 4(2): 155–164.
- Persson I-L, Wikan S, Swenson JE, and Myrsterud I. 2001. The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway. *Wildlife Biology* 7(1): 27–37.
- Piédallu B, Quenette P-Y, Mounet C, Lescureux N, Borelli-Massinés M, Dubarry E, Camarra J-J, and Gimenez O. 2016. Spatial variation in public attitudes towards brown bears in the French Pyrenees. *Biological Conservation* 197: 90–97.

BIBLIOGRAPHY

- Pop I-M, Bereczky L, Chiriac S, Iosif R, Nita A, Popescu VD, and Rozyłowicz L. 2018a. Movement ecology of brown bears (*Ursus arctos*) in the romanian eastern carpathians. *Nature Conservation* 26: 15–31.
- Pop I-M, Iosif R, Miu I V., Rozyłowicz L, and Popescu VD. 2018b. Combining resource selection functions and home-range data to identify habitat conservation priorities for brown bears. *Animal Conservation* 21(4): 352–362.
- Pritchard GT, and Robbins CT. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* 68(8): 1645–1651.
- Pyke GH, Pulliam HR, and Charnov EL. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* 52(2): 137–154.
- QGIS Development Team. 2020. QGIS Geographic Information System. <http://qgis.osgeo.org> (accessed 25 April 2020).
- R Core Team. 2020. R: a language and environment for statistical computing. version 4.0.2. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/> (accessed 24 June 2020).
- R Core Team. 2019. R: a language and environment for statistical computing. version 3.6.1. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/> (accessed 7 May 2020).
- Rode KD, Farley SD, and Robbins CT. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87(10): 2636–2646.
- Rodríguez C, Naves J, Fernández-Gil A, Obeso JR, and Delibes M. 2007. Long-term trends in food habits of a relict brown bear population in northern Spain: the influence of climate and local factors. *Environmental Conservation* 34(1): 36–44.
- Samson C, and Huot J. 1995. Reproductive biology of female black bears in relation to body mass in early winter. *Journal of Mammalogy* 76(1): 68–77.
- Sato Y, Aoi T, Kaji K, and Takatsuki S. 2004. Temporal changes in the population density and diet of brown bears in eastern Hokkaido, Japan. *Mammal Study* 29(1): 47–53.
- Sato Y, and Endo M. 2006. Relationship between crop use by brown bears and *Quercus crispula* acorn production in Furano, central Hokkaido, Japan. *Mammal Study* 31(2): 93–104.
- Sato Y, Itoh T, Mori Y, Satoh Y, and Mano T. 2011. Dispersal of male bears into peripheral habitats inferred from mtDNA haplotypes. *Ursus* 22(2): 120–132.
- Sato Y, Mano T, and Takatsuki S. 2005. Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan. *Wildlife Biology* 11(2): 133–144.
- Sato Y, Mano T, and Takatsuki S. 2000. Applicability of the point-frame method for

BIBLIOGRAPHY

- quantitative evaluation of bear diet. *Wildlife Society Bulletin* 28(2): 311–316.
- Schneider CA, Rasband WS, and Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9(7): 671–675.
- Schulte-Hostedde AI, Millar JS, and Hickling GJ. 2001. Evaluating body condition in small mammals. *Canadian Journal of Zoology* 79(6): 1021–1029.
- Schwartz CC, Fortin JK, Teisberg JE, Haroldson MA, Servheen C, Robbins CT, and Van Manen FT. 2014. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. *The Journal of Wildlife Management* 78(1): 68–78.
- Schwartz CC, Haroldson MA, and Cherry S. 2006. Reproductive performance of Grizzly Bears in the Greater Yellowstone Ecosystem, 1983-2002. *Wildlife Monographs* 161: 18–24.
- Schwartz CC, Keating KA, Reynolds, Harry V. I, Barnes, Victor G. J, Sellers RA, Swenson JE, Miller SD, McLellan BN, Keay J, McCann R, Gibeau M, Wakkinen WF, Mace RD, Kasworm W, Smith R, and Herrero S. 2003a. Reproductive maturation and senescence in the female brown bear. *Ursus* 14: 109–119.
- Schwartz CC, Miller SD, and Haroldson MA. 2003b. Grizzly bear, in: Thompson, B.C., Chapman, J.A. (Eds.), *Wild Mammals of North America: Biology, Management, and Conservation*. Johns Hopkins University Press, Baltimore, Maryland, U.S.A., pp. 556–586.
- Shimozuru M, Shirane Y, Tsuruga H, Yamanaka M, Nakanishi M, Ishinazaka T, Kasai S, Nose T, Masuda Y, Fujimoto Y, Mano T, and Tsubota T. 2019. Incidence of multiple paternity and inbreeding in high-density brown bear populations on the Shiretoko Peninsula, Hokkaido, Japan. *Journal of Heredity* 110(3): 321–331.
- Shimozuru M, Shirane Y, Yamanaka M, Nakanishi M, Ishinazaka T, Kasai S, Nose T, Shirayanagi M, Jimbo M, Tsuruga H, Mano T, and Tsubota T. 2020. Maternal human habituation enhances sons' risk of human-caused mortality in a large carnivore, brown bears. *Scientific Reports* 10(1): 16498.
- Shimozuru M, Yamanaka M, Nakanishi M, Moriwaki J, Mori F, Tsujino M, Shirane Y, Ishinazaka T, Kasai S, Nose T, Masuda Y, and Tsubota T. 2017. Reproductive parameters and cub survival of brown bears in the Rurua area of the Shiretoko Peninsula, Hokkaido, Japan. *PLOS ONE* 12(4): e0176251.
- Shirane Y, Mori F, Yamanaka M, Nakanishi M, Ishinazaka T, Mano T, Jimbo M, Sashika M, Tsubota T, and Shimozuru M. 2020. Development of a noninvasive photograph-based method for the evaluation of body condition in free-ranging brown bears. *PeerJ* 8: e9982.
- Shirane Y, Shimozuru M, Yamanaka M, Tsuruga H, Hirano S, Nagano N, Moriwaki J, Nakanishi M, Ishinazaka T, Nose T, Kasai S, Shirayanagi M, Masuda Y, Fujimoto Y, Osada M, Akaishi M, Mano T, Masuda R, Sashika M, and Tsubota T. 2018. Sex-biased

BIBLIOGRAPHY

- natal dispersal in Hokkaido brown bears revealed through mitochondrial DNA analysis. *European Journal of Wildlife Research* 64(6): 65.
- Shirane Y, Shimozuru M, Yamanaka M, Tsuruga H, Nakanishi M, Ishinazaka T, Nose T, Kasai S, Shirayanagi M, Masuda Y, Fujimoto Y, Mano T, Sashika M, and Tsubota T. 2019. Sex-biased dispersal and inbreeding avoidance in Hokkaido brown bears. *Journal of Mammalogy* 100(4): 1317–1326.
- Simard MA, Côté SD, Weladji RB, and Huot J. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. *Journal of Animal Ecology* 77(4): 678–686.
- Smith CC, and Follmer D. 1972. Food preferences of squirrels. *Ecology* 53(1): 82–91.
- Sollmann R, Tôrres NM, Furtado MM, De Almeida Jácomo AT, Palomares F, Roques S, and Silveira L. 2013. Combining camera-trapping and noninvasive genetic data in a spatial capture-recapture framework improves density estimates for the jaguar. *Biological Conservation* 167: 242–247.
- Spady TJ, Lindburg DG, and Durrant BS. 2007. Evolution of reproductive seasonality in bears. *Mammal Review* 37(1): 21–53.
- Stenset NE, Lutnæs PN, Bjarnadóttir V, Dahle B, Fossum KH, Jigsved P, Johansen T, Neumann W, Opseth O, Rønning O, Steyaert SMJG, Zedrosser A, Brunberg S, and Swenson JE. 2016. Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden. *Wildlife Biology* 22(3): 107–116.
- Steyaert SMJG, Endrestøl A, Hackländer K, Swenson JE, and Zedrosser A. 2012. The mating system of the brown bear *Ursus arctos*. *Mammal Review* 42(1): 12–34.
- Steyaert SMJG, Leclerc M, Pelletier F, Kindberg J, Brunberg S, Swenson JE, and Zedrosser A. 2016. Human shields mediate sexual conflict in a top predator. *Proceedings of the Royal Society B: Biological Sciences* 283(1833): 20160906.
- Steyaert SMJG, Swenson JE, and Zedrosser A. 2014. Litter loss triggers estrus in a nonsocial seasonal breeder. *Ecology and Evolution* 4(3): 300–310.
- Stirling I, and Derocher AE. 1993. Possible impacts of climatic warming on polar bears. *Arctic* 46(3): 240–245.
- Stirling I, Pearson AM, and Bunnell FL. 1976. Population ecology studies of polar and grizzly bears in northern Canada. *Transactions, Forty-First North American Wildlife and Natural Resources Conference, March 21-25, 1976, Washington, D.C.* 41: 421–429.
- Stirling I, Thiemann GW, and Richardson E. 2008. Quantitative support for a subjective fatness index for immobilized polar bears. *Journal of Wildlife Management* 72(2): 568–574.
- Støen O-G, Bellemain E, Sæbø S, and Swenson JE. 2005. Kin-related spatial structure in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology* 59(2): 191–197.

BIBLIOGRAPHY

- Su J, Aryal A, Hegab IM, Shrestha UB, Coogan SCP, Sathyakumar S, Dalannast M, Dou Z, Suo Y, Dabu X, Fu H, Wu L, and Ji W. 2018. Decreasing brown bear (*Ursus arctos*) habitat due to climate change in Central Asia and the Asian Highlands. *Ecology and Evolution* 8(23): 11887–11899.
- Swenson JE, Adamič M, Huber D, and Stokke S. 2007. Brown bear body mass and growth in northern and southern Europe. *Oecologia* 153(1): 37–47.
- Swenson JE, and Haroldson MA. 2008. Observations of mixed-aged litters in brown bears. *Ursus* 19(1): 73–79.
- Swenson JE, Sandegren F, Brunberg S, Segerström P, and Segerstrøm P. 2001. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12: 69–80.
- Tarugara A, Clegg BW, Gandiwa E, Muposhi VK, and Wenham CM. 2019. Measuring body dimensions of leopards (*Panthera pardus*) from camera trap photographs. *PeerJ* (7): e7630.
- Tukey J. 1977. Exploratory data analysis. Addison-Wesley Publishing Co., Reading, Boston, U.S.A.
- Urabe H, Mishima Y, and Miyakoshi Y. 2013. Evaluation of spawning habitat for chum and masu salmon in Tokachi River basin (Note) (in Japanese). *Scientific reports of Hokkaido Fisheries Research Institutes* 84: 47–56.
- Vulla E, Hobson KA, Korsten M, Leht M, Martin A-J, Lind A, Männil P, Valdmann H, and Saarma U. 2009. Carnivory is positively correlated with latitude among omnivorous mammals: Evidence from brown bears, badgers and pine martens. *Annales Zoologici Fennici* 46(6): 395–415.
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, and Bairlein F. 2002. Ecological responses to recent climate change. *Nature* 416(6879): 389–395.
- Ware J V., Nelson OL, Robbins CT, Carter PA, Sarver BAJ, and Jansen HT. 2013. Endocrine rhythms in the brown bear (*Ursus arctos*): Evidence supporting selection for decreased pineal gland size. *Physiological Reports* 1(3): e00048.
- Welch CA, Keay J, Kendall KC, and Robbins CT. 1997. Constraints on frugivory by bears. *Ecology* 78(4): 1105–1119.
- Wildman EE, Jones GM, Wagner PE, Boman RL, Troutt Jr HF, and Lesch TN. 1982. A Dairy Cow Body Condition Scoring System and Its Relationship to Selected Production Characteristics. *Journal of Dairy Science* 65(3): 495–501.
- Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*.

BIBLIOGRAPHY

- Series B: Statistical Methodology* 73(1): 3–36.
- Wright PA, Obbard ME, Battersby BJ, Felskie AK, LeBlanc PJ, and Ballantyne JS. 1999. Lactation during hibernation in wild black bears: Effects on plasma amino acids and nitrogen metabolites. *Physiological and Biochemical Zoology* 72(5): 597–604.
- Yamanaka A. 2011. Study on evaluation methods for nutritional and reproductive conditions of the Japanese black bear (*Ursus thibetanus japonicus*) using samples from carcasses (in Japanese). Hokkaido University, Sapporo, Hokkaido, Japan.
- Yamanaka M, and Aoi T. 1988. Brown bears (in Japanese), in: Ohtaishi, N., Nakagawa, H. (Eds.), *Animals of Shiretoko*. Hokkaido University Press, Sapporo, Hokkaido, Japan, pp. 181–223.
- Yoneda M. 1976. Age determination and age structure of the Ezo brown bear. *The Journal of the Mammalogical Society of Japan* 7(1): 1–8.
- Young RA. 1976. Fat, energy and mammalian survival. *American Zoologist* 16(4): 699–710.
- Zalewska K, and Zalewski A. 2019. Size selection of alternative prey relative to the abundance of primary prey: Pine marten hunting for frogs. *Annales Zoologici Fennici* 56(1–6): 41–49.
- Zedrosser A, Dahle B, and Swenson JE. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87(3): 510–518.
- Zedrosser A, Steyaert SMJG, Gossow H, and Swenson JE. 2011. Brown bear conservation and the ghost of persecution past. *Biological Conservation* 144(9): 2163–2170.
- Zuur AF, Ieno EN, Walker N, Saveliev AA, and Smith GM. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, U.S.A

SYNOPSIS (IN JAPANESE)

ヒグマは日和見的な雑食動物であり、食物資源の季節的および年次的な変動や空間的な差異に応じて採餌食物を変化させる。北海道北東部に位置する知床半島では、ヒグマが高脂質食物であるハイマツの実や高タンパク食物であるカラフトマスを利用しているが、それらの採食量が年によって異なるのかは明らかでない。本研究では、ヒグマの食性の季節的および年次的な変動を明らかにすること、またそれらの変動がヒグマの栄養状態や行動様式にどのように影響するのかを明らかにすることを目的とした。

第 1 章では、野生のヒグマの栄養状態を長期的にモニタリングすることを可能にするために、写真を用いて栄養状態を評価する非侵襲的な方法を開発した。本研究では、多くの哺乳類で確立されている Body Condition Index (BCI) を真の栄養状態の基準値として採用した。まず、1998～2017 年に知床半島において有害駆除や狩猟などによって捕殺された個体の実測値を用いて予備的検討を行った。その結果、春には BCI が低く、秋には高くなるという季節変化がみられた。また、胴高-体長比と BCI との間に強い相関がみられたことから、胴高-体長比が栄養状態評価指標として有用であることが示された。次に、半島先端部に位置するルシャ地区において継続して観察可能なメス成獣 1 個体をモデル動物として、写真を用いた計測精度の検証を行った。2017 年 9 月 24～26 日に計 220 枚の横向きの写真を撮影し、ヒグマの姿勢（胴部の真直度や頸部の傾き）によって写真を分類した。4 種類の計測手法を用いて胴高-体長比あるいは胴高-胴長比を算出し、それらの値がヒグマの姿勢によって変化するかを調べた。その結果、最も多様なヒグマの姿勢に適用することができ、かつ計測のばらつきが十分に小さい手法は、胴高-胴長比 (TH:HTL) であることが明らかとなった。また同じ 1 個体について、2016～2018 年の 6～10 月に撮影された写真を用いて TH:HTL を算出した結果、TH:HTL が春や夏に比べて秋に有意に高くなり、栄養状態の季節変化を反映することが確認された。最後に、ルシャ地区において生体捕獲された 7 個体の実測値から BCI を算出し同じ 7 個体の写真から算出した TH:HTL との相関を調べた。その結果、両者の間に有意な相関がみられたことから、写真を用いて正確な栄養状態評価が可能であることが示された。

第 2 章では、食性の季節的および年次的な変動や繁殖状況によってメス成獣ヒグマの栄養状態がどのように変化するのかを明らかにするために、2012～2018 年にルシャ地区において長期的な調査を行った。まず、2,079 サンプルのヒグマの糞を分析したところ、ハイマツが 8 月の推定エネルギー摂取量の 39.8% を、サケ科魚類が 9 月の 46.1% を占めていることが明らかとなり、さらにそれらの摂取量が年によって大きく変化することが示された。次

に、第1章で開発した方法を用いて、12個体の成獣メスの1,226枚の写真から栄養状態を評価した。その結果、栄養状態は6月から8月下旬まで悪化し続け、サケ科魚類が利用可能となる9月に回復し始めた。また、ハイマツとサケ科魚類の採食量がともに多い年には、栄養状態が回復し始める時期が早くなることが明らかとなった。さらに、子連れのメスは単独のメスよりも栄養状態が悪く、特にサケ科魚類の採食量が少ない年には悪化が顕著になることが示された。

第3章では、メス成獣が繁殖状況および食物環境によってどのように行動を変化させるのかを明らかにするために、ルシャ地区において7個体の成獣メスにGPS首輪を装着した。本研究では、0歳子の運動能力の低さによって、子連れのメスでは食物資源の獲得が制限されているのではないかと仮説を立てた。まず、1時間あたりに移動する速度を算出した結果、子連れのメスは単独のメスよりも移動速度が遅いことが示された。また、植生や傾斜といった環境要因も移動速度に影響しており、傾斜が急な場所や高標高のハイマツ帯では移動速度が遅くなることが明らかとなった。次に、資源選択関数を用いて各季節の生息地選択性を調べた結果、子の有無にかかわらず、晩夏にはハイマツ帯を強く選択していることが明らかとなった。一方で、ハイマツの消費量が少なかった年には、子連れ個体および単独個体ともにハイマツ帯を避ける傾向があった。最後に、1日を日中・薄明薄暮・夜間の3つの時間帯に分類し、それぞれの時間帯においてヒグマがサケ科魚類の遡上河川を訪れる確率を算出した。その結果、河川を訪れる時間帯には繁殖状況による有意な差がなかった。以上の結果から、子連れのメスは移動が制限されているものの、ハイマツやサケ科魚類の利用においては単独のメスと明確な違いはないことが示された。

本研究により、ハイマツとサケ科魚類がヒグマの栄養状態および行動様式を決定する鍵食物であることが明らかとなった。限られた期間に高山帯のハイマツと海岸のサケ科魚類という環境の全く異なる食物資源に依存しているという点は、知床半島におけるヒグマのユニークな生態を表している。また、これらの食物を十分に利用できない年には、栄養状態が悪化し、行動様式も変化させることが明らかとなった。知床半島では、夏に食物不足がヒグマの人里への出没につながっているのではないかと考えられており、本研究で得られた発見が、人とヒグマの軋轢を引き起こすメカニズムの解明につながることを期待される。ヒグマの生態のさらなる理解と効率的な保護管理を実現するためには、性齢クラスなど個体によってどのように食性が異なるのか、また食物資源量の地域差がヒグマの行動様式にどのように影響するのかを解明する、さらなる研究が求められる。