

BEHAVIOR-SPECIFIC RESOURCE SELECTION
BY KODIAK BROWN BEARS

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ABSTRACT

For many coastal brown bear (*Ursus arctos middendorffi*) populations throughout Alaska and British Columbia, bears are subject to changes due to increases in human activity. The world renowned productivity and size of brown bears on Kodiak National Wildlife Refuge (NWR) has, no doubt, helped to increase tourism within the Refuge over the last decade. This increase in human pressure within ecologically sensitive areas has the potential to displace native species, such as the brown bear. Identifying factors that influence patterns of space use and habitat selection by bears is an important first step to developing a management and conservation strategy that could incorporate increased human activity as well as wildlife needs.

Our first objective was to identify the factors that influence patterns of habitat selection by brown bears when foraging. To better evaluate this habitat selection within a behavioral context, we used both movement and activity data collected from GPS-collared bears to identify locations associated with foraging behavior. To more accurately identify the timing and use of important food items that influence space use, we estimated food habitats by collecting fecal samples from bed sites used by GPS-collared individuals. We found that the distribution of temporally varying food items consistently affected patterns of space use by bears. During the spring, active bears selected areas that were lower in elevation and received higher amounts of solar radiation where new growth from herbaceous vegetation would be prevalent. Early in the summer when salmon became available within the study site, bears selected areas closer to streams where salmon spawned. Later in the fall, bears selected habitat types with high occurrence of both important berry-producing shrubs and northern groundcone (*Boschniakia rossica*). We quantified patterns of space use by active

bears that are driven by seasonally abundant foods, and this study facilitated an analysis that revealed underlying factors that motivate and limit animal movements and space use.

Our second objective was to identify the factors that influence selection patterns of bedding sites by brown bears across multiple scales. Again, we used both movement and activity data collected from GPS-collared bears to identify locations associated with bedding behavior. We proposed three ecological hypotheses that might motivate decisions about bedding habitat, and we used information theoretic criteria to evaluate each hypothesis at each scale. We found that at the largest scale (home range), the availability of food was the most important factor influencing habitat selection at bedding sites, while at the finest scale (micro-site), factors that influence thermal regulation or conspecific avoidance were the most important, depending on maternal status. Following Rettie and Messier's (2000) hypothesis, which states that the most limiting factors should affect habitat selection at the largest scales, we posit that bottom up resources (i.e., food) appear to be the most limiting factor influencing individual fitness of brown bears on Kodiak as compared to top down pressures (i.e., shelter or risk).

Our third objective was to develop and test a pilot protocol for quantifying salmon escapement on Karluk Lake tributaries. We used an autonomous video system to enumerate salmon passing both upstream and downstream at 2 streams. We estimated the total escapement for 12 days at Canyon Creek and 10 days at Meadow Creek. In general, salmon moved upstream during the daytime and downstream during nocturnal periods. Future studies investigating salmon movements and abundance should consider additional variability according to time of day, as well as seasonal trends in abundance.

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THESIS INTRODUCTION

The conservation of brown bears (*Ursus arctos middendorffi*) is a high-profile wildlife management issue throughout North America. For many coastal populations throughout Alaska and British Columbia, bears are subject to changes due to increases human activity (Rode, Farley & Robbins 2006b). The world renowned productivity and size of bears on Kodiak National Wildlife Refuge (NWR) has, no doubt, helped to increase tourism within the Refuge over the last decade (U.S. Fish and Wildlife Service 2007). In addition, the native corporation, Koniag, initiated a bear viewing program in 2011 and expanded infrastructure to accommodate the operation. This program will be run under the guidance of Kodiak NWR, however, an increase in human pressure to ecologically sensitive areas has the potential to displace native species, such as the brown bear. Identifying the factors that influence patterns of space use and habitat selection by brown bears is an important first step to developing a management and conservation strategy that could incorporate increased human activity as well as wildlife needs. In addition to proximate concerns, long-term natural and anthropogenic changes, including climate change, have the potential to dramatically alter the spatial distribution and temporal availability of key resources, and a clearer understanding of these dynamic patterns will improve managers' ability to predict responses of brown bears to future changes.

In heterogeneous and dynamic environments, animals select different habitats to fulfill different life-history objectives. Unfortunately, many studies investigating space use by animals often do not differentiate among locations that are used by an animal to satisfy different life-history requirements or locations that are used incidentally (Beyer *et al.* 2010). Interpreting occupancy as a homogenous form of use limits our understanding of the

mechanisms that influence space use and likely provides less insightful results about habitat features that promote fitness of individuals and persistence of populations. To improve our understanding of wildlife-habitat relationships, a critical area for research is connecting actual behaviors of animals to data collected from telemetry (Hebblewhite & Haydon 2010).

Understanding space use and patterns of habitat selection for many reclusive and wide-ranging species, such as ocean-going fish, migratory birds, and long-distance migratory mammals, have been aided by the advancement of GPS technologies (e.g., Hamer *et al.* 2009; Sawyer & Kauffman 2011). Coupled with improvements in GIS and spatial analyses, researchers can build models that are better able to predict animal distributions. Although GPS technology has allowed researchers to collect animal movement data at fine temporal scales, a lack of comparable resolution for resources that vary widely in availability across time and space has hindered our ability to identify ecological patterns (Hebblewhite & Haydon 2010).

The goal of our work was to use both GPS location data and activity data to quantify behavior-specific habitat selection by brown bears. In the first chapter, we developed an approach that enhanced our ability to use GPS location data to estimate behavior-specific patterns of habitat selection by a large-bodied omnivore while foraging on resources that vary in availability over space and time. To more accurately identify the timing and use of important food items that influence space use, we estimated food habitats by collecting fecal samples from bed sites used by GPS-collared individuals. In the second chapter, we examined resources that influence selection patterns at bedding sites across multiple spatial scales. We used a rule-based algorithm to identify bed sites used by female bears using both activity and movement data. We were particularly interested in examining the relative

importance of food availability, thermal regulation, and factors that might reduce risk of aggressive encounters with conspecifics and potentially infanticide by male bears. In the third chapter, we developed a field protocol that allowed us to estimate salmon abundance at the tributary level at a finer temporal resolution. We used an automated video system to record salmon movements both entering and exiting the stream and retrospectively enumerated salmon within each system.

By linking GPS telemetry locations with behaviors and using additional biological information to define how use of resources varied over time, we demonstrate an approach for how GPS data and remotely sensed habitat data can be used to more precisely assess the influence of resources on behavior-specific patterns of space use and habitat selection. This approach facilitates a better understanding about how large and wide-ranging omnivores like Kodiak brown bears meet their resource needs and how variation in individual strategies might shape patterns of habitat selection within a population.

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CHAPTER 1:

Using diet analyses to inform behavior-specific models of resource selection by foraging brown bears

SUMMARY

1. Patterns of space use by animals are commonly evaluated using GPS technologies and remotely sensed habitat data. However, such information often limits inferences about animal behavior, and it provides little information about how dynamic patterns of resource availability might influence patterns of space use. We developed an approach that enhanced our ability to use GPS location data to estimate behavior-specific patterns of habitat selection by a large-bodied omnivore while foraging on resources that vary in availability over space and time.
2. We conducted a diet analysis for brown bears (*Ursus arctos middendorffi*) on Kodiak Island, Alaska, to define timing and magnitude of use of different foods, and we used both movement and activity data to distinguish animal behaviors. We then used these data to inform models that evaluated spatial and temporal patterns of habitat selection by 30 adult female bears.
3. As expected, while bears were active (i.e., not bedding), the distribution of food resources strongly influenced their patterns of space use and habitat selection within their home range. At the population level, brown bears selected for lower elevation areas that received greater solar radiation where new vegetative growth was available during the spring. Summer and autumn foraging areas were closer to streams with available salmon, and later in autumn when the abundance of salmon declined, bears selected areas with

greater abundance of berry-producing shrubs and northern ground-cone. Selection of resources varied markedly among individuals, however, likely related to maternal status and differing strategies for optimizing mass gains.

4. The disconnect between animal behavior and analyses of resource selection that frequently results from remotely sensed data weakens our ability to understand factors that motivate animal space use. Our work illustrates an approach that linked behavior of a wide-ranging omnivore to GPS location data for evaluation of selection of temporally varying resources. Inclusion of additional biological data, such as diet and activity, to GPS-based analyses of resource selection can enhance our ability to understand the processes that shape patterns of animal space use.

Key-words: Alaska, behavior, brown bears, diet, foraging, habitat selection, Kodiak, salmon, space use, synoptic model, *Ursus arctos middendorffi*

INTRODUCTION

Patterns of space use by animals emerge, in part, from the behavioral process of selection for resources that meet their life history requirements. In addition, individuals must balance tradeoffs among competing resource needs, such as acquiring food, seeking shelter, and rearing offspring (Godvik *et al.* 2009; Hebblewhite & Merrill 2009; Mabelle *et al.* 2012). Spatial and temporal distribution and availability of resources that meet those needs have a primary influence on how animals use space (Eide, Jepsen & Prestrud 2004). Consequently, understanding why and how individuals select resources, and how quality and availability of resources vary across space and time, are fundamental to advancing our understanding of factors that shape patterns of space use by animals.

A common approach to testing hypotheses about how resources influence patterns of space use is to contrast use and availability of resources to draw conclusions about habitat selection. Many studies of resource selection, however, have not defined use within a behavioral context (Godvik *et al.* 2009; Beyer *et al.* 2010). Thus, the results are limited because they only represent the average selection of resources across all behaviors, even though resources selected during differing behavioral states such as foraging and resting are likely to differ markedly (Cooper & Millsbaugh 2001). Quantifying the links between animal behavior and resource decisions that motivate space use will advance our understanding of the processes that govern the spatial ecology of animals (Beyer *et al.* 2010; Hebblewhite & Haydon 2010).

Understanding space use and patterns of habitat selection for many reclusive and wide-ranging species, such as ocean-going fish, migratory birds, and long-distance migratory mammals, has been aided by the advancement of GPS technologies (e.g., (Hamer *et al.* 2009; Sawyer & Kauffman 2011). Coupled with improvements in GIS and spatial analyses, researchers can build models that are better able to predict animal distributions. Although GPS technology has allowed researchers to collect animal movement data at fine temporal scales, a lack of comparable resolution for resources that vary widely in availability across time and space has hindered our ability to identify ecological patterns (Hebblewhite & Haydon 2010). Many studies have examined patterns of resource selection across more than one time period (e.g., month, season, or year); however, such temporal categories often only approximate how availability of resources changes over time, and it is unlikely that availability of important resources correlate through time and space.

Our goal was to develop an approach that more accurately quantified resource selection by a wide-ranging species during foraging when availability of foods varied markedly in space and time. The brown bear (*Ursus arctos middendorffi*) is an ideal model species for examining how behavior-specific resource selection shapes patterns of movements and space use, especially foraging behaviors. Due to nutritional constraints imposed by hibernation and a relatively inefficient digestive physiology, these large-bodied omnivores maximize weight gain, and ultimately fitness, by spending the majority of their time either foraging or resting (MacHutchon 2001). Because the immediate resource needs of a foraging bear (i.e., food) are not the same as the needs of a resting bear (shelter or security), a variety of habitat resources are used by individuals throughout a day to satisfy these contrasting needs (Munro *et al.* 2006; Moe *et al.* 2007). Using GPS-collar technology, researchers have reported accurate identification of animal locations associated with bedding behavior by brown bears (Sorum 2013; Ch. 2). By excluding animal locations associated with bedding behavior, we can more effectively identify the mechanisms that influence habitat selection by brown bears within the context of foraging.

We used animal locations gathered from GPS-collared female brown bears on Kodiak Island, Alaska, to evaluate the influence of temporally and spatially dynamic forage distributions on patterns of space use and habitat selection. We quantified diet to identify important forage items and timing of use of these foods, and we used these data to model the spatial and temporal distribution of food resources. Because brown bears are large omnivores with high energy requirements, we expected that (H1) while bears are active, the distribution of food resources strongly influences their patterns of space use and habitat selection, particularly food items that are either highly nutritious (e.g., salmon) or important

in optimizing macronutrient intake to maximize the efficiency of mass gain (Robbins *et al.* 2007). However, because bears are omnivorous and opportunistic feeders, we also expected that (H2) variation in patterns of space use and habitat selection among individuals would reflect differing foraging strategies within the population. By linking GPS telemetry locations with behaviors and using additional biological information to define how use of resources varied over time, we demonstrate an approach for how GPS data and remotely sensed habitat data can be used to more precisely assess the influence of resources on patterns of space use and habitat selection. This approach facilitates a better understanding about how large and wide-ranging omnivores like Kodiak brown bears meet their dietary needs and how variation in foraging strategies might shape patterns of habitat selection by individuals.

METHODS

Study Area

We evaluated forage-site selection (defined below) by female brown bears in the southwestern portion of the Kodiak Island, Alaska, centered on Karluk Lake (Fig. 1.1). The area is characterized by broad valleys, steep slopes, and mountain peaks up to approximately 950 meters. The climate is sub-arctic maritime, characterized by wet conditions and cool temperatures.

We radio collared bears within the southwestern region of the Kodiak National Wildlife Refuge (KNWR) and adjacent U.S. Fish and Wildlife Service (USFWS) conservation easement lands owned by Koniag Native Corporation. Lowland habitats were a mix of bog and marshlands, willow-grass-forb communities, ericaceous shrub and heath

communities, and cottonwood (*Populus balsamifera*) and birch (*Betula kenaica*) communities, which dominated river courses and low-elevation drainages in the eastern portion of the study area. Mid-elevation slopes were dominated by Sitka alder (*Alnus crispa*) and patches of European red elderberry (*Sambucus racemosa*). Openings in tall shrub habitat were typically occupied by low shrub and herbaceous cover. The alpine zone (>500 m) was characterized by dwarf shrub and low willow (*Salix* spp.), heath communities, herbaceous meadows, bare soil, and rock. Human recreational activity in this region was uncommon and mostly confined to larger lakes and river courses for the purposes of rafting, fishing, bear viewing, and hunting. Brown bears were hunted during both the spring (9 Apr – 15 May) and autumn (25 Oct – 15 Nov) seasons.

Six species of Pacific salmon (*Oncorhynchus* spp.) spawn in the study area, with about 3.09 million and 1.15 million individuals present during 2010 and 2011, respectively (Foster 2011; Moore 2012). Timing of salmon runs varied by species, beginning during late May and continuing through October (Foster 2011; Moore 2012). Based on abundance, the dominant ungulate was the introduced Sitka black-tail deer (*Odocoileus hemionus sitkensis*), followed by introduced mountain goats (*Oreamnos americanus*). Dominant berry species present within the study area included salmonberry (*Rubus spectabilis*) and elderberry, which produce ripe fruits between August and October. These berry species generally occurred within the alder matrix at elevations below 500 m. Other vegetation common in bear diets included nootka lupine (*Lupinus nootkatensis*), horsetails (*Equisetum* sp.), cow parsnip (*Heraculum lanatum*), *Angelica* sp., grasses, and sedges.

Animal Capture and GPS telemetry

We captured female brown bears and fitted them with GPS telemetry collars during June 2010 and 2011. Bears were darted from a helicopter and immobilized with Telazol (1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride; Fort Dodge Animal Health, Fort Dodge, Iowa, USA) at a concentration of 228.8 mg/ml. We fitted bears with GPS telemetry collars (Telonics Model #TGW-3790) programmed to obtain a location every hour from 15 May to 15 November; this period encompassed the majority of the year when bears were out of hibernation. Collars also were equipped with VHF transmitters that we used to locate individuals from fixed-wing aircraft for remote download of GPS data. We conducted telemetry flights weekly from early June through late October, weather permitting, and downloaded GPS data from the previous download date to the current date. We screened the GPS location data to eliminate large location errors; data screening was based on two- and three-dimensional (2D and 3D) GPS fixes in relation to the positional dilution of precision (PDOP); 3D positions having a PDOP >10 and 2D positions having a PDOP >5 were removed following recommendations of Lewis *et al.* (2007). The remnant GPS error was small ($\pm 10\text{m}$; *unpublished data*). Activity sensors in the GPS collars were programmed to record the proportional amount of time (in seconds) that a bear's head was in the downward position ($\geq 15^\circ$ below horizontal) during the 5-minute period immediately after a GPS location was recorded. We considered this measure as an index to the proportion of time spent feeding and/or moving (Schwartz *et al.* 2009). The animal capture and handling protocol followed standard techniques for this species and were approved by the IACUC of the Alaska Department of Fish and Game (Protocol No. 07-08). In addition, all methods

conform to the guidelines of the American Society of Mammalogists for use of wild mammals in research (Sikes & Gannon 2011).

To facilitate analyses of habitat selection during foraging, we first used both movement patterns and data from the activity sensors to partition the GPS locations into those associated with bedding versus active behaviors. We identified bedding locations using a rule-based algorithm developed in R (R Development Core Team 2011) that included 2 criteria: 1) ≥ 3 “low activity” sequential locations, thereby ensuring a duration of >2 hours of resting behavior; and 2) ≤ 20 m between sequential resting locations, which was equal to approximately twice the error rate of the GPS-collars (Sorum 2013; Ch. 2). GPS locations were considered low activity (e.g., resting or standing) if a measurement of $\leq 15\%$ was recorded by the activity sensor (Schwartz *et al.* 2009). The data set used in our analyses included all GPS locations for bears considered to be active (i.e., not bedded).

Diet Analysis

We analyzed fecal samples to quantify forage items in the diet and to identify timing of use of the different foods in our study area to approximate when those foods became available to bears. Bears often defecate around the edges of their bed sites, and we collected fresh feces at bedding sites that had been used by GPS-collared individuals during 8 June – 12 October of 2011. The common behavior of prolonged bedding bouts allowed us to both identify bedding locations of collared individuals and to collect feces associated with the respective bedding bouts. We randomly selected 8 of our collared bears and visited their bedding sites throughout the season to collect fecal samples. If a collar malfunctioned (i.e., no or limited location data were collected) or prematurely deployed (i.e., bear died or slipped

the collar), then we randomly selected another collared bear so that we maintained a sample size of ≥ 6 collared individuals at all times.

To obtain a representative sample of diet patterns of brown bears throughout the field season, we selected and then visited one bedding site per individual every 2 days. Two-person teams used hand-held GPS units to navigate to the sites where they conducted systematic searches for evidence of the bed site and feces. Evidence of recent bedding, such as excavated ground or depressed vegetation, was used to identify bed sites, and if multiple bed sites were evident, then we selected the bed closest to the putative bedding location based on GPS collar data (Sorum 2013; Ch. 2). We collected recent bear feces of an age that corresponded with the date when the bedding event occurred, and we attributed the feces to the GPS-collared individual. Only feces that were determined to have been deposited within approximately 2 weeks were collected. This was based on characteristics of the scat, including a relatively dark and moist interior with an exterior that was often drier and lighter colored. If multiple fresh fecal samples were found at a bed site, we collected only one sample unless they appeared to contain markedly different foods, in which case, we collected all recently deposited fecal samples from the site. All fecal samples were frozen until subsequent analyses of diet were performed. For overall assessments of diet at the population level, fecal samples from adults were pooled across individuals for each 2-week period. We also examined fecal samples for each individual separately to evaluate diet at the individual level.

We quantified the relative contribution of food items within each fecal sample. Samples were thawed in 1 L of water and rinsed in a 2-mm sieve until only macroscopic components remained. Subsamples were drawn, transferred to a shallow pan, and examined

microscopically. Undigested food remains were identified to the finest taxonomic resolution possible. We estimated relative percentage by volume of each food item. Correction factors developed by Hewitt & Robbins (1996) were applied to account for biases in differences of recognizable fecal residue produced by different foods; these ratios were used to convert estimated relative volumes to actual relative food habits (e.g., Fortin *et al.* 2013).

Analysis of Space Use and Habitat Selection

At the home range scale, we estimated habitat selection by active female brown bears at the individual level using the synoptic model of space use (Horne, Garton & Rachlow 2008). This approach uses a weighted distribution to simultaneously model an individual's space use and habitat selection that influences its space use (Johnson *et al.* 2008; Forester, Im & Rathouz 2009). Under this approach, the probability density of being at spatial location x , a vector of x and y coordinates, is

$$f_u(x, t) = \frac{f_a(x) \times w(x, t)}{\int f_a(x) \times w(x, t)} \quad (1)$$

where $f_a(x)$ is the null distribution of space use, which models the probability of use in the absence of habitat selection, and $w(x, t)$ is a resource selection function that transforms $f_a(x)$ to $f_u(x, t)$ by selectively weighting areas based on habitat conditions. The denominator in the equation is a normalizing constant for a weighted distribution that ensures $f_u(x, t)$ is a probability density function that integrates to 1. We defined the resource selection function as

$$w(x, t) = \text{Exp}[H(x)' \beta P(t)] \quad (2)$$

where $H(x)$ is a vector of covariate values describing the habitat or environmental conditions at location x , β is a vector of parameters (i.e., selection coefficients) to be estimated, and $P(t)$ is an interaction term representing functions of time to allow for temporal variation in habitat

selection (Ferguson, Taylor & Messier 2000; Forester, Im & Rathouz 2009). We defined $f_a(x) = BVN(\theta)$ to be a stationary (i.e., time invariant) bivariate normal distribution with parameters θ describing the means and variances in the x and y dimensions and the covariance. We used maximum likelihood (via numerical optimization) to estimate the parameters governing the null model of home range (θ) and the selection coefficients (β) with a program written in R (R Development Core Team 2011).

We restricted our analysis to the period between 1 June and 15 October, because this was approximately the period for which we were able to systematically collect fecal samples, and thus infer use of food items. This study period also avoided the potentially confounding factors of den site location and hunting seasons (early spring and late autumn), which likely influence space use by bears in our study area. For individuals that we observed during both years ($n = 9$), we combined data for a single analysis of space use because the annual home range of these individuals were relatively similar.

Habitat Models

We used results from the diet analysis to develop habitat models that represented the spatio-temporal distribution of important food resources, which we used to examine patterns of space use and habitat selection by active bears. We assumed that categories of foods (vegetative material, salmon, berries and roots) were available in our study area when they appeared in the diets of bears. Because use of food items was dynamic through time, we investigated habitat selection and space use as a function of foraging strategies that varied across time with use and availability of forage resources. We used remotely sensed data to quantify spatial distributions of foods across time periods defined by the diet analysis.

New vegetative growth is an important food item during the spring and summer for many bear populations (Miller & Glenn 1980; Servheen 1983; Waller & Mace 1997; Rode, Farley & Robbins 2006b). During the spring, we expected that habitat features that facilitate snowmelt, such as increasing solar radiation and lower elevation, would promote growth of vegetation. Specifically, we expected selection to increase with decreasing elevation and increasing solar radiation index (SRI). Therefore, we included an interaction term P_{spring} for these covariates, which equaled 1 if time-of-year was 1 June – 24 June and 0 if otherwise. During the summer, delayed plant emergence and rapid rates of plant growth have been suggested to influence space use by brown bears (Atwell *et al.* 1980), and these conditions are promoted in higher elevation alpine sites (Körner 1989; Fox 1991). Thus, we also expected bears in our study to forage on vegetation at higher elevations during the summer. Therefore, we included an interaction term P_{summer} for this covariate, which equaled 1 if time-of-year was 25 June – 15 August and 0 if otherwise. The variables of SRI and elevation were derived from a digital elevation model (DEM) (Table 1.1). The SRI was a function of slope, aspect, and latitude (Keating *et al.* 2007), and values were greatest for south-facing, moderate slopes and least for steep, northern aspects.

Because of the extensive use and nutritional importance of salmon (*Oncorhynchus sp.*) to brown bears (Barnes 1990; Hilderbrand *et al.* 1999; Belant *et al.* 2006), we expected bears to use areas close to streams with salmon during the salmon runs. The locations of all streams with salmon were derived from an Alaska Department of Fish and Game database (*ADF&G unpublished data*). We determined the distance to nearest stream with salmon using the NEAR function in ArcGIS 10 (Environmental Systems Research Institute, Redlands, California). Because lake shorelines also are important salmon foraging areas for brown

bears (Barnes 1990), we also considered these areas as available for foraging on salmon by including all waters <133 m from the shoreline, which was the distance that encompassed 95% of non-terrestrial bear locations.

Because of the suspected importance of fall berries and roots (Clark 1957; Fortin *et al.* 2007), we used a detailed description of Kodiak Island vegetation (Fleming & Spencer 2007) and a vegetative community assessment estimated at bear locations (Appendix 1) to identify land cover classes most likely to be associated with occurrence of both berry-producing shrubs and northern groundcone (*Boschniakia rossica*). Because northern groundcone are holoparasitic and often parasitize alders, we included cover types that contained alder. We consolidated 10 of the 64 distinct cover types into one, *berry.root*, which represented the distribution of the vegetative fall foods described above.

Before modeling resource selection, we screened predictor variables for collinearity. We assumed that if $|r| < 0.60$, then correlation was not a concern between predictor covariates (Sawyer *et al.* 2006; Ciarniello *et al.* 2007), and none of our variables were considered correlated based on this criterion. We aggregated all raster-based covariates to a 90-m² resolution to facilitate computation of the synoptic model across the large home ranges. To account for temporal variation in habitat selection, we included interaction terms between selection coefficients (i.e., the β 's in equation 2) and functions of time (Ferguson, Taylor & Messier 2000; Forester, Im & Rathouz 2009).

Model Selection

We used an information-theoretic approach for evaluating synoptic models of habitat selection (Burnham & Anderson 2002). Because we hypothesized that space use and habitat selection by active bears is largely influenced by the distribution of food, we developed a set

of *a priori* models that included time-varying habitat variables that describe the spatiotemporal distribution of food items: 1) green vegetation, 2) salmon, and 3) berries and northern groundcone. We developed 7 candidate models that included combinations of these variables representing the distribution of each food item (Table 1.2). Because brown bears can demonstrate considerable individual variation in diet patterns (Hilderbrand *et al.* 1999; Belant *et al.* 2006; Edwards *et al.* 2011), we fit models to location data for each individual. We ranked the models for each bear using the difference in AIC_c values from the model with the smallest AIC_c value (ΔAIC_c), and determined the relative likelihood of each model using Akaike weights (Burnham & Anderson 2002).

We evaluated selection of habitat at both the individual and population levels. For individual-level inferences, we averaged each parameter estimate ($\hat{\beta}$) across models based on Akaike weights. We first scaled the weights to sum to 1 across models containing each variable because the same variables did not occur in all 7 models (Burnham & Anderson 2002). For population-level inferences, we averaged parameter estimates ($\hat{\beta}$) across individuals. For a conservative measure of precision, we considered a coefficient to be significant if 2 times the standard error of the mean did not contain zero (Boyce 2006; Fieberg *et al.* 2010).

RESULTS

We captured 30 female brown bears (20 adults that were not accompanied by young, 2 adults with cubs >1 year of age, 2 adults with cubs of the year, and 6 subadults) during early June of 2010 and 2011. We identified 18.1 % of 85,114 total GPS locations as associated with bedding behavior, and those location data were excluded from analyses of potential

forage site selection. Consequently, we conducted analyses of foraging site selection with a total 69,697 non-bedding (i.e., active) locations from 30 individuals. Nine individuals were collared in both years, and we combined data for a single analysis of space use per individual. The maternal status of 2 of those females changed between years, and in those cases, we only retained data from the year when they were accompanied by cubs.

We visited 375 putative bed sites from 12 individuals (mean bed/bear = 31.3) and found strong evidence of recent bedding activity at 365 sites (Sorum 2013; Ch. 2). On average, used bed sites were 6.7 m (SE = 0.3) from the putative location identified using the rule-based algorithm (Sorum 2013; Ch. 2). We collected fresh fecal samples at 283 bed sites (mean scats/bear = 23.6, SE = 3.5) throughout all seasons: we collected 51 scats from 8 individuals (mean scat/bear = 6.8, SE = 0.8) during spring; 127 scats from 9 individuals (mean scat/bear = 14.1, SE = 1.7) during summer; 84 scats from 7 individuals (mean scat/bear = 12.0, SE = 1.6) during early autumn; and 21 scats from 6 individuals (mean scat/bear = 3.5, SE = 0.6) during late autumn.

Diet Analysis and Model Development

Diets of brown bears in our study were diverse and highly variable through time. Green vegetation, which included graminoids, horsetails (*Equisetum spp.*), and forbs, dominated spring to mid-summer diets and decreased markedly thereafter (Fig. 1.2a). The most frequently consumed forbs during late spring and early summer were cow parsnip (*Heracleum lanatum*), *Anglica spp.*, stinging nettle (*Urtica lyallii*), and lupine (*Lupinus nootkatensis*). Salmon first appeared in the diet of bears in our study area in early July, and use of this food item increased throughout the summer and peaked in mid-September before decreasing (Fig. 1.2b). The average bimonthly proportion of salmon in the diet of bears prior

to and after August 15th was approximately 17% and 63%, respectively (Table 1.2). Berries became more prevalent in the diet of bears as they began to ripen during autumn (August 16 – October 15). Two berry species contributed >99% of all berries identified in the feces: salmonberry and elderberry (Fig. 1.2c). Also, northern groundcone (*Boschniakia rossica*), a parasitic plant of the broom-rape family (*Orobanchaceae*), began appearing in the diet of bears after 1 October and contributed to 24% of the diet (Fig. 1.2c). The average bimonthly proportion of both of these food items, berries and groundcone, in the diet of bears was greater after 1 October (56%) than before (13%).

The diet analysis helped to identify timing in use of important categories of food items, and we incorporated this temporal information into the models (Tables 1.1 and 1.3) to better understand how diet influenced space use patterns by bears. Based on the diet analysis, salmon were available from early July through mid-October, and use of salmon increased after August 15 (Fig. 1.2b), suggesting that the influence of salmon on space use by bears might differ between the two periods. Therefore, we estimated selection for each period separately, and we expected that although bears would select for areas in proximity to streams during both periods, the effect would be greatest during the fall when the proportion of salmon in the diet of bears was highest. To examine this relationship, we included the interaction terms $P_{salmon.early}$ and $P_{salmon.late}$ for this covariate, which equaled 1 if time-of-year was 1 July–15 August or 16 August–15 October, respectively, and 0 if otherwise. In addition, use of berries and northern groundcone during the fall appeared to differ, thus we expected selection for habitat types that contained salmonberry, elderberry, and/or northern groundcone throughout the fall, but because the bimonthly average proportion of these food items in the diet was greater after 1 October than before, we expected the effect on space use

by bears to be greatest after 1 October. To examine this relationship, we included the interaction terms $P_{fall.early}$ and $P_{fall.late}$ for this covariate, which equaled 1 if time-of-year was 15 August–1 October and 1 October–15 October, respectively, and 0 if otherwise.

Population-level Habitat Selection

At the home range scale, the distribution of bears when active, and presumed foraging, was best described by the resource selection models representing the spatial and temporal distribution of each of the major categories of food in their diet (i.e., green vegetation, salmon, and berries and roots). These results suggested that bears adjusted patterns of space use through time to accommodate availability of a diversity of food items. The selection model that included variables that estimated distribution of all 3 foods (Comprehensive Model) consistently outperformed models that included variables associated with only 1 or 2 of the food categories (Table 1.4). Furthermore, across all individuals for which the Comprehensive Model was ranked the highest (28 of 30 bears), that model received, on average, 99.8% of the AICc weight with no other models within 6 AICc, suggesting strong model performance among these individuals (Table 1.4).

Graminoids and forbs dominated the diet of bears during the spring and remained important throughout the summer, and as expected, distribution of fresh graminoids and forbs (herbaceous vegetation) also strongly influenced space use by foraging bears at the population level. We modeled distribution of herbaceous vegetation using parameters for solar radiation and elevation, and both influenced probability of habitat selection. During the spring when snow covered vegetation at moderate to high elevations, average probability ratios indicated that every 100-m increase in elevation resulted in a 20% decrease in selection, and that a 10% increase in the solar radiation index resulted in a 34% increase in

selection; these results indicated that bears selected areas with features that promoted snowmelt and advanced plant phenology during spring (Table 1.5). Contrary to expectations that bears would select higher elevations during summer where the receding snowline provides access to fast-growing, young shoots from herbaceous vegetation, bears continued to exhibit selection for lower elevations at the population level. Average probability ratios indicated that every 100 m of additional elevation resulted in a 21% decrease in selection. However, during the summer, multiple food resources such as herbaceous vegetation and salmon were consumed by bears, and there was considerable variation in foraging strategies among individuals.

The importance of salmon resources on habitat selection during summer and autumn was evident in space use relative to streams. Average probability ratios indicated that every 100 m of additional distance from streams resulted in a 15% and 25% decrease in selection during summer and autumn, respectively (Table 1.5). Bears foraged in closer proximity to streams during both seasons, but concentrations were greatest during the autumn when salmon consumption was highest (Fig. 1.2b).

Bears began consuming berries during early August, and the proportion of berries increased within their diet throughout the autumn. Roots of the northern groundcone became an important component of the diet after 1 October, and they occurred at relatively high levels thereafter in the diets of bears in our study. Average probability ratios indicated that prior to 1 October, bears were approximately 0.42 times as likely to select habitat types associated with berries and northern groundcone (*berry.root*) compared to habitats without these resources, but after 1 October, they were 1.15 times as likely to select *berry.root*. Averaged across individuals, bears spent a higher proportion of their time in *berry.root*

habitat after 1 October (44%, SE = 5, range = 8 – 75 %) than before (21%, SE = 3, range = 4 – 82 %). Overall, these results suggested that foraging bears selected against habitats associated with berries and northern groundcone prior to 1 October, and weakly selected for those habitats thereafter. Although use of berries and roots as reflected in the diet and time spent in the *berry.root* habitat was high during the autumn, selection for this habitat was low likely because of its widespread availability.

Individual-level Habitat Selection

Although the Comprehensive Model was the best supported model across all bears, there was considerable variation among individuals with regard to the parameter estimates. The probability ratios varied widely across animals (Table 1.5), suggesting that foraging strategies were highly variable among individuals. For example, individuals varied in their selection patterns of elevation during the summer. Although most bears (96.7%) selected areas closer to streams during this time, approximately $\frac{3}{4}$ of these individuals selected areas lower in elevation (average probability ratio = 0.74), while nearly $\frac{1}{4}$ selected areas higher in elevation (average probability ratio = 1.22). These results suggested that the larger group remained in lower elevation areas foraging on herbaceous vegetation and salmon, while the smaller group traveled between streams, where they foraged on salmon, and the alpine areas adjacent to streams, where they foraged on newly emerging vegetation. Examination of individual diet patterns corroborated this assertion. We estimated the diet of 8 bears that selected for areas closer to streams, of which 6 selected against higher elevation, while 2 selected for higher elevation. While the average proportion of salmon was nearly equal between bears that selected against (18.0%) and for (15.5%) elevation, the average proportion of Nootka lupine, an important bear food that occurs more commonly in the

alpine habitat within our study area (Sorum 2013; Ch. 2), was considerably lower for bears that selected against elevation (3%) in contrast to those that selected for higher elevations (15%).

Our investigations of space use at the individual level also revealed variation in selection of patterns of *berry.root* after 1 October. One group of 11 females weakly selected against *berry.root* (average probability ratio = 0.57), while another group of 12 females selected for *berry.root* (average probability ratio = 2.88). Six of those individuals were included in our diet analyses, 3 that selected against and 3 that selected for *berry.root* habitat. Average diet composition of berries and northern groundcone for those individuals that selected against and for *berry.root* habitat was <1.0% and 90.3%, respectively. Again, individual-level space use and diet analysis provided complementary results that supported the contention that population-level parameter estimates might not accurately depict forage selection across all individuals.

We also detected variation in space use patterns at the individual level that were likely correlated with factors other than availability of food resources. For example, during the spring while the population selected against areas higher in elevation, females with cubs of the year strongly selected for these areas, and their estimated average use of elevation (636m) was more than double that of the rest of the population (296m). These results suggested that maternal status, and specifically vulnerability of young cubs, influenced space use, and that examination of habitat use and selection by individuals revealed patterns not detected in the population-level analysis.

DISCUSSION

We combined two analyses to evaluate how distribution of food resources influenced habitat selection by a large omnivore in a novel way that allowed us to overcome some of the inherent limitations of remotely sensed location data gathered from wide-ranging animals. We conducted an analysis of food habits to define timing and magnitude of use of different foods by female brown bears, and then we used those data to inform models that evaluated spatial and temporal patterns of habitat selection. In addition, our use of behavior-specific locations allowed a more rigorous test of habitat selection by foraging individuals. By incorporating these analyses into the synoptic modeling approach, we evaluated how the distribution of food resources simultaneously shaped space use and habitat selection at both the population and individual levels. Overall patterns of selection of forage resources were similar across individuals, yet variation in parameter estimates among individuals suggested that some bears employed different foraging strategies, which we explored qualitatively using information about individual diets.

Because habitat use by animals is likely to differ markedly among behaviors (e.g., foraging, bedding, rearing young), studies investigating habitat selection should incorporate information on behavior (Cooper & Millspaugh 2001; Beyer *et al.* 2010). Researchers have commonly partitioned locations into time periods, such as times of day, that are likely to be correlated with different behaviors, however, this requires an *a priori* understanding of variation in diel activity (Moe *et al.* 2007). We addressed this issue in our study by directly linking a behavioral state to the animal locations using both movement and activity criteria. Consequently, we believe that our model more precisely reflects habitat selection by female brown bears while foraging. Sampling space use within the context of a behavioral process

improves the ability to make inferences about the process, and therefore, to develop a deeper understanding of the underlining mechanisms that govern animal movements and distributions (Beyer *et al.* 2010).

One of the primary challenges for studies investigating habitat selection is defining what resources are available to the animals and how best to quantify availability across time and space in ways that accurately reflect the nature of the biological system (Wheatley & Johnson 2009). We demonstrated that this obstacle can be overcome by estimating the diet composition of GPS-collared female brown bears through time and using this information to define the temporal availability of each food item separately. Although the diet data represent use rather than availability *per se*, we reasoned that if bears were using a particular forage item, that it was by definition, available to be used at that time. Employing this approach, we were able to focus our analysis of resource selection by more accurately representing food items available to the population, and results are more likely to represent the selection process.

At the population level, we predicted (H1) that distribution of temporally varying food items would consistently affect patterns of space use by bears throughout the active season. As expected, habitat selection by bears in our study indicated that the distribution of herbaceous vegetation strongly influenced patterns of space use during the spring. Early in the season, lower elevation areas that received higher amounts of solar radiation were important to foraging bears. Similarly, the movement patterns and habitat use of both coastal (Miller & Glenn 1980; Titus *et al.* 1999) and interior (Servheen 1983; Waller & Mace 1997; Ciarniello *et al.* 2007) brown bears also were influenced by plant phenology during spring. We also hypothesized that bears would select areas during the summer that promoted delayed

plant phenology and rapid plant growth, and that higher elevation areas would be selected primarily for this reason (Atwell *et al.* 1980; Titus *et al.* 1999). Contrary to our expectations, higher elevations were still selected against during the summer, however, these results were likely influenced by availability of abundant salmon beginning in July (Fig. 1.2b). Salmon is an important food resource for many bear populations during summer (Jacoby *et al.* 1999; Hilderbrand *et al.* 1999), including ours (Fig. 1.2b), and consequently, use of lower elevations at that time was likely influenced by proximity to streams and lake shores, which occurred at lower elevations within the study area.

As expected, at the population level bears selected areas closer to streams while salmon were available and the effect of selection was greatest during the fall when salmon were most abundant within the study area. The population-level diet analysis and parameter estimates from the habitat selection models both indicated that salmon were even more highly sought after during the autumn compared to the summer. Given the spatial accuracy at which we could identify the distribution of salmon resources (i.e., streams), it is not surprising that we were able to detect both strong habitat selection and temporal differences in relative strength of selection.

A surprising finding of our study was the prevalence of the northern groundcone in the late autumn diet of brown bears on Kodiak Island. To our knowledge, our study is the first to document use of northern groundcone exceeding 25% digestible dry matter for any brown bear population, however, we caution quantitative interpretation of these results due to a small number of individuals in our diet sample at that time of the year ($n = 6$). During autumn, berries also made up a significant proportion of diet at the population level (approximately 15%), a phenomenon that has been documented for many coastal brown bear

populations (Hamilton & Bunnell 1987; McCarthy 1989; Fortin *et al.* 2007). Although salmon were still available to bears through mid-October, some individuals appeared to leave spawning streams to consume both fruit and northern groundcone. Robbins *et al.* (2007) found that both wild and captive bears attempted to regulate total protein, energy, and carbohydrate intake by consuming a mixed diet of salmon and berries, which maximized energy intake and mass gain. Therefore, it is likely that some individuals in our study may have benefited, as well, by following a similar strategy.

Although overall selection of forage resources was consistent at the population level, evaluation of individual-level selection revealed variation across bears. In some cases, such variation resulted from differences in foraging strategies among individuals, while others were likely motivated by factors other than foraging behavior. For example, selection of elevation varied among individuals during the summer, even though most individuals selected areas closer to streams. Selection of areas both higher in elevation and closer to streams by some individual bears probably resulted from their use of higher elevation areas during periods of low salmon abundance. Salmon are highly variable in abundance and timing of availability even during the spawning season (Deacy & Leacock 2012), and socially dominant bears can displace other bears along streams, particularly when salmon abundance is low (Gende & Quinn 2004). Thus, it is possible that during periods of low salmon availability, the alpine environment provided a predictable location for abundant and highly nutritious vegetative food resources (Atwell *et al.* 1980). These areas might be of particular importance during years or periods of depressed salmon abundance or for individuals that might not have access to salmon streams due to social or maternal status (Ben-David, Titus & Beier 2004; Rode, Farley & Robbins 2006a; Fortin *et al.* 2007). Other

studies investigating movements and habitat use by coastal brown bears have documented bears remaining in the alpine and never using salmon resources even when they were available (Schoen, Lentfer & Beier 1986). Because plant materials are energetically less nutritious than salmon (Pritchard & Robbins 1990), and the relatively large body size of brown bears imposes energetic demands and constraints, it is unlikely that most individuals could maintain a plant-based diet (Rode, Robbins & Shipley 2001). Nonetheless, the alpine areas during summer appear to be important foraging areas for some individuals, and the resources there likely helped bears meet nutritional demands, particularly, during periods of lower salmon availability.

Similarly, we documented considerable variation among individuals in selection for berries and northern groundcone, particularly after 1 October. As the abundance of salmon began decreasing later in the autumn, selection of *berry.root* habitat by some individuals likely resulted from a transition into a more plant-based diet. For those bears, it is possible that a diet dominated by berries and roots became more advantageous due to the spatial predictability of and nutrition provided by those food items. Other individuals, however, selected against *berry.root* habitat and likely continued foraging on salmon later into the autumn.

Following the approach by Sorum (2013; Ch. 2), we were able to exclude nearly 20% of bear locations from our analyses of foraging habitat selection due to their high likelihood of being associated with extended bedding behavior (≥ 2 hrs). But, we were unable to omit locations that were created while bears were resting for brief periods (i.e., < 2 hrs), and therefore, these locations had the potential to influence our habitat selection analyses. Resting sites used for brief periods, however, were likely selected due to their proximity to

foraging areas because bears often rest for short durations between intensive bouts of foraging. We frequently observed foraging bears stop feeding, construct a bed, and briefly rest in the same habitat, only to resume foraging within an hour. In these instances, the mechanisms driving space use at these short-term resting sites were likely more related to forage availability than shelter or security. Nonetheless, future studies examining space use patterns of foraging animals may want to consider using additional techniques, such as animal-borne video, that could provide a higher resolution link between space use and behavior by animals (Moll *et al.* 2007).

Habitat selection patterns also revealed variation among individuals unrelated to forage availability. We observed selection of higher elevations areas during the spring by females with cubs of the year. Several studies have reported that females with cubs remained at higher elevations during the spring (Miller & Glenn 1980; Milakovic *et al.* 2012), and it is likely that such selection is related to security rather than forage requirements (Dahle & Swenson 2003). Indeed, other factors such as reproductive status or body condition also likely affect space use of some individuals, and examination of resource use and selection at the individual level will enhance our ability to discover the mechanisms that shape behavior-specific patterns of habitat use.

Remotely sensed animal locations and habitat data provide researchers with powerful tools for examining distribution and habitat selection by wide-ranging species. The remote nature of the data collection, however, can result in a disconnect between an animal's biology and a researcher's analyses of resource selection (Hebblewhite & Haydon 2010).

Developing and applying methods that more precisely link behavior to animal locations gathered via GPS or other remote technology will improve the ability of models of space use

to accurately predict the distribution of animals. Furthermore, sampling space use within the context of a behavioral process will enhance our ability to make inferences about the processes that drive the patterns (Beyer *et al.* 2010). Use of additional biological data (e.g., diet information or activity data) can help refine dynamic patterns of resource availability, and together, these methods will facilitate analyses that reveal underlying factors that motivate and limit animal movements and space use.

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Table 1.1. Description of spatial ($H(x)$) and temporal ($P(t)$) model parameters and specific covariates in each models evaluating habitat selection by active female brown bears during foraging in southwestern Kodiak Island, Alaska, USA.

Model Parameters	Specific Covariates	Description
$H(x)$	SRI	Solar radiation index as a function of slope, aspect, and latitude (Keating et al. 2007)
	elev	Elevation above sea level (m)
	berry.root	Land cover map depicting the distribution of important berries and roots
	dist.stream	Distance (m) to nearest salmon stream
$P(t)$	spring	1 June - 24 June
	summer	25 June - 14 August
	fall.early	15 August - 31 September
	fall.late	1 October - 15 October
	salmon.early	1 July - 14 August
	salmon.late	15 August - 15 October

Table 1.2. Description and expected direction of relationships between selection and habitat variables in the *a priori* candidate models used to evaluate habitat selection by active brown bears in southwest Kodiak Island, Alaska, USA.

Model	Working Hypothesis	Model Structure	Expected Results
1 Green Vegetation	Distribution of fresh growth from forbs and graminoids influences habitat selection.	$(\beta_1 \times P_{\text{spring}})\text{SRI} + (\beta_2 \times P_{\text{spring}})\text{elev} + (\beta_3 \times P_{\text{summer}})\text{elev}$	$\beta_1 > 0, \beta_2 < 0, \beta_3 > 0$
2 Berries/Roots	Distribution of berries and roots influences habitat selection.	$(\beta_1 \times P_{\text{fall.early}})\text{berry.root} + (\beta_2 \times P_{\text{fall.late}})\text{berry.root}$	$\beta_1 > 0, \beta_2 > 0$
3 Fish	Spawning salmon influence habitat selection.	$(\beta_1 \times P_{\text{salmon.early}})\text{dist.stream} + (\beta_2 \times P_{\text{salmon.late}})\text{dist.stream}$	$\beta_1 < 0, \beta_2 < 0$
4 Green Vegetation & Berries/Roots		$(\beta_1 \times P_{\text{spring}})\text{SRI} + (\beta_2 \times P_{\text{spring}})\text{elev} + (\beta_3 \times P_{\text{summer}})\text{elev} + (\beta_4 \times P_{\text{fall.early}})\text{berry.root} + (\beta_5 \times P_{\text{fall.late}})\text{berry.root}$	$\beta_1 > 0, \beta_2 < 0, \beta_3 > 0, \beta_4 > 0, \beta_5 > 0$
5 Green Vegetation & Fish		$(\beta_1 \times P_{\text{spring}})\text{SRI} + (\beta_2 \times P_{\text{spring}})\text{elev} + (\beta_3 \times P_{\text{summer}})\text{elev} + (\beta_4 \times P_{\text{salmon.early}})\text{dist.stream} + (\beta_5 \times P_{\text{salmon.late}})\text{dist.stream}$	$\beta_1 > 0, \beta_2 < 0, \beta_3 > 0, \beta_4 < 0, \beta_5 < 0$
6 Fish & Berries/Roots		$(\beta_1 \times P_{\text{salmon.early}})\text{dist.stream} + (\beta_2 \times P_{\text{salmon.late}})\text{dist.stream} + (\beta_3 \times P_{\text{fall.early}})\text{berry.root} + (\beta_4 \times P_{\text{fall.late}})\text{berry.root}$	$\beta_1 < 0, \beta_2 < 0, \beta_3 > 0, \beta_4 > 0$
7 Comprehensive	All food items influence habitat selection.	$(\beta_1 \times P_{\text{spring}})\text{SRI} + (\beta_2 \times P_{\text{spring}})\text{elev} + (\beta_3 \times P_{\text{summer}})\text{elev} + (\beta_4 \times P_{\text{salmon.early}})\text{dist.stream} + (\beta_5 \times P_{\text{salmon.late}})\text{dist.stream} + (\beta_6 \times P_{\text{fall.early}})\text{berry.root} + (\beta_7 \times P_{\text{fall.late}})\text{berry.root}$	$\beta_1 > 0, \beta_2 < 0, \beta_3 > 0, \beta_4 < 0, \beta_5 < 0, \beta_6 > 0, \beta_7 > 0$

Table 1.3. Percent (%) bimonthly estimated food habits (FH) of female brown bears living in southwestern Kodiak Island, Alaska, USA, based on the percentage of major food items found in feces when corrected for differential disappearance (Hewitt and Robbins 1996). Fecal samples (*n*) were collected from bed sites of collared individuals during 2011. Also, percent (%) frequency (*f*) of each food item is provided.

Period	n	Grasses		Horsetails		Sedges		Forbs		Fruits		Roots		Fish		Ungulates		Miscellaneous	
		% FH	% <i>f</i>	% FH	% <i>f</i>	% FH	% <i>f</i>	% FH	% <i>f</i>	% FH	% <i>f</i>	% FH	% <i>f</i>	% FH	% <i>f</i>	% FH	% <i>f</i>	% FH	% <i>f</i>
Early June	20	35	95	10	45	15	65	25	60	0	0	0	0	0	0	5	5	10	40
Late June	46	16	83	12	57	11	72	47	85	0	0	0	0	0	0	8	15	4	37
Early July	41	16	68	19	56	14	76	43	76	0	0	2	7	5	2	0	0	1	27
Late July	46	15	85	11	72	19	87	32	95	0	3	4	10	15	15	2	3	2	36
Early August	38	10	76	6	42	18	84	19	76	5	8	6	21	33	37	0	3	2	37
Late August	34	3	71	11	32	2	62	7	47	16	32	6	24	54	53	0	3	1	35
Early September	17	1	65	0	12	1	59	0	41	12	12	0	6	87	88	0	6	0	24
Late September	21	5	71	0	0	0	67	2	67	12	19	1	29	80	81	0	0	0	24
Early October	20	5	35	0	0	2	25	7	30	21	50	35	60	30	30	0	0	1	5

Table 1.4. The number of individuals for which each model of habitat selection by foraging brown bears received the most support at southwestern Kodiak Island, Alaska, USA.

Hypothesis	No. individuals	Akaike wt	
		Avg	Range
1. Null	0		
2. Green Vegetation	0		
3. Berries & Roots	0		
4. Fish	0		
5. Green Vegetation & Fish	2	0.788	0.734-0.842
6. Green Vegetation & Berries/Roots	0		
7. Fish & Berries/Roots	0		
8. Comprehensive	28	0.998	0.965-1.00

Table 1.5. Average parameter estimates and probability ratios used to describe the habitat selection by 30 foraging female brown bears on Kodiak Island, Alaska, USA.

Food Item	Covariates	β (average)	SE	Prob Ratio (average)	Prob Ratio (interquartile range)
Green	$P_{spring} \times SRI^a$	2.18	1.38	1.32 (10%)	(0.76, 1.75)
Vegetation	$P_{spring} \times elev^b$	-2.69	1.17	0.81 (100m)	(0.59, 1.00)
	$P_{summer} \times elev^b$	-2.73	1.00	0.80 (100m)	(0.59, 1.07)
Salmon	$P_{salmon.early} \times dist.stream^b$	-19.25	3.74	0.85 (100m)	(0.11, 0.80)
	$P_{salmon.late} \times dist.stream^b$	-32.17	6.18	0.75 (100m)	(0.68, 0.89)
Berry & Roots	$P_{fall.early} \times root.berry^c$	-0.88	0.17	0.40	(0.23, 0.76)
	$P_{fall.late} \times root.berry^c$	0.17	0.16	1.24	(0.72, 2.80)

^a - Probability ratio represents how selection changes with 10% increase in solar radiation.

^b - Probability ratio represents how selection changes for every increase in 100m.

^c - Probability ratio represents how selection differs in *berry.root* habitat compared to outside of this vegetation type.

Note: Bold values indicate significance across all animals.

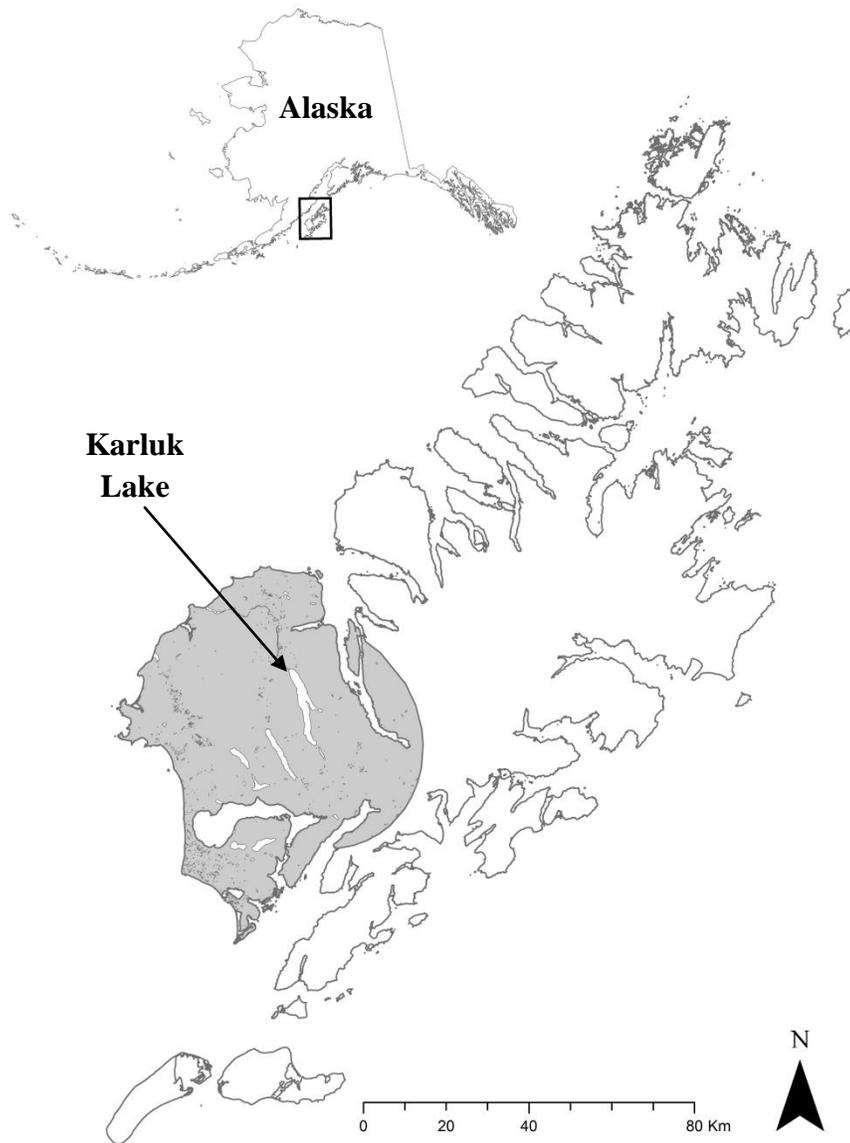


Figure 1.1. The study area (gray) encompassing southwestern Kodiak Island, Alaska, which is set within the Gulf of Alaska, USA.

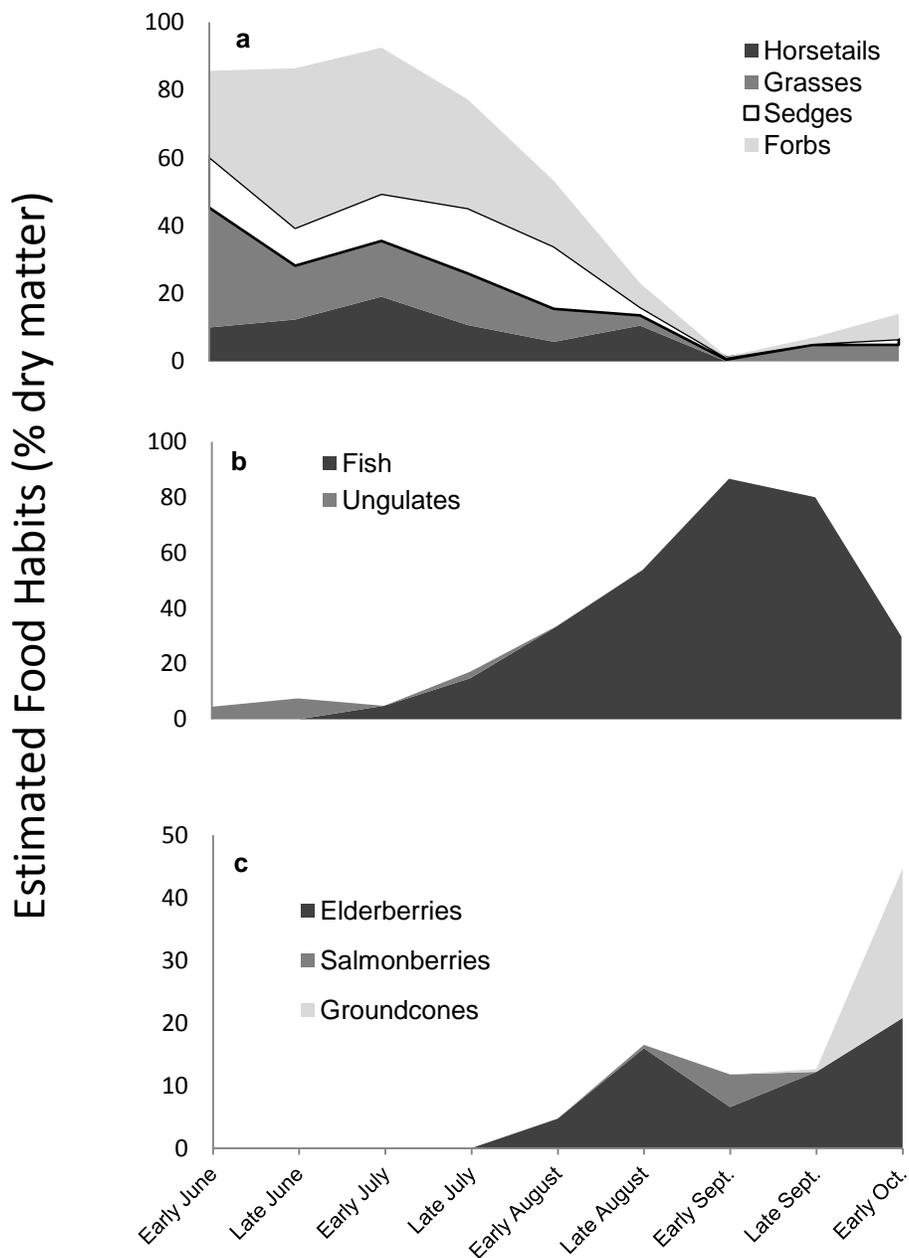


Figure 1.2. Estimated food habits of female brown bears living in southwestern Kodiak Island, Alaska, USA, during 2011 based on the percentage of 3 categories of food items found in feces when corrected for differential disappearance (Hewitt and Robbins 1996): a) green vegetation, b) meat, c) berries and northern groundcone.

CHAPTER 2:

Hierarchical bed site selection by Kodiak brown bears

SUMMARY

1. Factors that influence patterns of selection by individuals can vary across scale, and therefore, wildlife-habitat relationships should be examined across a range of scales to identify limiting factors influencing animal space use. In addition, patterns of habitat selection are likely to vary among behaviors; however, many studies investigating space use by animals have not differentiated among locations that are used to satisfy different life-history requirements or locations that are used incidentally.
2. We used movement and activity data to identify bed sites used by GPS-collared female brown bears (*Ursus arctos middendorffi*) on Kodiak Island, Alaska, USA. We then evaluated spatial and temporal patterns of habitat selection across multiple scales by 30 female bears to identify factors influencing selection of bedding habitat.
3. At the scale of the home range, the distribution of food resources strongly influenced patterns of space use and habitat selection during bedding, suggesting that availability of food items was the most important limiting factor across the population. At the finest spatial scale (i.e., area immediately surrounding the bed site), factors that influence both thermal regulation and security were the most important resources influencing space use, however, selection of these factors also appeared to be influenced by maternal status.
4. Patterns of space use by animals are complex and driven by varying life-history objectives, yet remotely-sensed locations rarely provides information about what the animal is doing. By increasing the behavioral resolution of the animal location data, we

were able to gain insight into the underlying mechanisms that govern selection of bed sites across spatial scales and evaluate which factors are potentially most limiting to brown bears on Kodiak Island.

Key-words: Alaska, bed, behavior, brown bears, conditional logistic regression, habitat selection, Kodiak, limiting factor, resource selection, scale, space use, synoptic model, *Ursus arctos middendorffi*

INTRODUCTION

Resource selection is a hierarchical process of behavioral responses of animals to habitat characteristics. Factors that influence patterns of selection by individuals can vary across scale, and therefore, wildlife-habitat relationships should be examined across a range of scales to identify limiting factors influencing animal space use (Wiens *et al.* 1986; Boyce 2006). In addition, patterns of habitat selection are likely to vary among behaviors because animals use different resources to fulfill different life-history requirements, such as resting, foraging, and rearing young. Many studies investigating space use by animals, however, have not differentiated among locations that are used to satisfy different life-history requirements or locations that are used incidentally (Beyer *et al.* 2010). Interpreting occupancy as a homogenous form of use limits our understanding of the mechanisms that influence space use and likely provides less insightful results about habitat features that promote fitness of individuals and persistence of populations (Beyer *et al.* 2010; Kertson & Marzluff 2010). Although data from global positioning system (GPS) telemetry can improve our understanding of wildlife-habitat relationships, a critical area for research is connecting statistical and actual behaviors from GPS telemetry location data (Hebblewhite & Haydon

2010). Such techniques will facilitate identification of behavior-specific patterns of habitat selection.

GPS-based location data have been linked with animal behavior using cluster analysis, which has proven to be an effective method for identifying behaviors that produce longer occupancy within relatively small spatial areas. Cluster analysis was used to estimate kill rates by cougars (*Puma concolor*; Anderson & Lindzey 2003) and subsequently, to identify locations of kills by large carnivores including cougars (Knopff *et al.* 2009), wolves (*Canis lupus*) in both Scandinavia (Sand *et al.* 2005, 2008) and North America (Webb, Hebblewhite & Merrill 2008), and African lions (*Panthera leo*; Tambling *et al.* 2010). Resting behavior by many species likely exhibits similar spatiotemporal patterns, and cluster analysis techniques also might be useful for identifying bedding or resting sites.

Additional information regarding activity of an animal could markedly improve our ability to distinguish telemetry locations associated with bedding behavior compared to active behaviors (i.e., traveling or foraging; Moe *et al.* 2007; Schwartz *et al.* 2009). Recent advances in motion sensor technology integrated within GPS transceivers have provided more reliable tools for studying activity patterns of animals. In some cases, however, measurements of activity might not be reliable indicators of specific behaviors (Gervasi, Brunberg & Swenson 2006), particularly when measurements of activity are not near the extremes of high or low levels (Schwartz *et al.* 2009). Consequently, research evaluating the link between data from activity sensors and animal behavior could be improved by combining activity data with analyses of movement patterns from GPS telemetry data. Together, these techniques could advance our understanding of behavior-specific space use and habitat relationships.

The goal of our work was to use both GPS location data and activity data to quantify behavior-specific habitat selection by brown bears (*Ursus arctos middendorffi*). Our first objective was to build and evaluate an approach that accurately identified sites associated with bedding behavior by female bears using both location and activity data collected via GPS collars. Our second objective was to identify the resources that influence selection of bed sites by female brown bears across spatial scales. We were particularly interested in examining the relative importance of food availability, thermal regulation, and factors that might reduce risk of aggressive encounters with conspecifics and potentially infanticide by male bears.

We evaluated support for 3 ecological hypotheses (forage, thermal, and security) that might explain observed patterns of space use and bed site selection by female brown bears. First, because the ability to acquire seasonally abundant nutritious forage plays an important role in habitat selection by bears (Munro *et al.* 2006; Belant *et al.* 2009; Nielsen *et al.* 2010; Milakovic *et al.* 2012), we evaluated whether seasonal distribution of important bear foods influenced bed site selection (Forage Availability Hypothesis). Second, because bears are well adapted to cooler environments due to their large body size and effective insulation (Øritsland 1970; Best 1982), we predicted that risk of overheating also would influence selection of bed sites during the day. To test this prediction, we developed the Thermal Regulation Hypothesis, which included covariates that influence the amount of direct sunlight reaching the surface of the earth. Third, female bears are considered subordinate to males, and in some populations, patterns of habitat selection differ between the sexes (McLoughlin *et al.* 2002; Rode, Farley & Robbins 2006a; Ciarniello *et al.* 2007b). In addition, females with cubs have been observed to avoid preferred habitats (e.g., streams

with salmon) with high male densities to reduce risk of infanticide (Ben-David, Titus & Beier 2004; Rode, Farley & Robbins 2006a). Therefore, we included the Conspecific Avoidance Hypothesis that predicts that bears would use habitat characteristics when bedded that reduce the risk of surprise encounters by increasing their ability to detect approaching conspecifics.

Because habitat selection by animals is a hierarchical process occurring across spatial and temporal scales (Johnson 1980; Wiens *et al.* 1986), and this process has been documented in bear populations (Ciarniello *et al.* 2007b), we examined the influence of each hypothesis for habitat selection across 3 complimentary scales: home range, local, and micro-habitat. Rettie & Messier (2000) suggested that patterns of habitat selection should permit animals to attain the most limiting factors at the largest scales, while less important limiting resources should influence habitat selection at finer scales. Brown bears are large-bodied omnivores with high annual nutritional requirements that must be obtained during 6 to 7-month active periods. In addition, in southwestern Kodiak Island, these apex predators are subject to few anthropogenic structures (e.g., roads) that could increase risk of human-caused mortality (Suring & Del Frate 2002; Ciarniello *et al.* 2007a; Martin *et al.* 2012). Hence, fitness is likely to be limited by bottom-up resources (i.e., food) more than top-down limitations (i.e., conspecific aggression, infanticide, or human-caused mortality). Thus, we expected (H1) that selection of bed sites would be influenced by forage availability at the largest spatial scale, and that selection would be driven by more immediate needs, such as thermoregulation and conspecific avoidance at the finer scales. In addition, we expected (H2) that patterns of habitat selection would differ among individuals as a function of individual resource requirements (e.g., maternal status). Our study demonstrates an approach for investigating

important behavior-specific requirements (i.e., bedding habitat) across spatial scales in the context of multiple competing hypotheses to improve our understanding of the factors that govern animal space use.

METHODS

Study Area

We evaluated bed-site selection (defined below) by female brown bears in the southwestern portion of the Kodiak Island, Alaska, centered on Karluk Lake (Fig. 2.1). The area is characterized by broad valleys, steep slopes, and mountain peaks up to approximately 950 meters. The climate is sub-arctic maritime, characterized by wet conditions and cool temperatures.

We radio collared bears within the southwestern region of the Kodiak National Wildlife Refuge (KNWR) and adjacent U.S. Fish and Wildlife Service (USFWS) conservation easement lands owned by Koniag Native Corporation. Lowland habitats were a mix of bog and marshlands, willow-grass-forb communities, ericaceous shrub and heath communities, and cottonwood (*Populus balsamifera*) and birch (*Betula kenaica*) communities, which dominated river courses and low-elevation drainages in the eastern portion of the study area. Mid-elevation slopes were dominated by Sitka alder (*Alnus crispa*) and patches of European red elderberry (*Sambucus racemosa*). Openings in tall shrub habitat were typically occupied by low shrub and herbaceous cover. The alpine zone (>500 m) was characterized by dwarf shrub and low willow (*Salix* spp.), heath communities, herbaceous meadows, bare soil, and rock. Human recreational activity in this region was uncommon and mostly confined to larger lakes and river courses for the purposes of rafting, fishing, bear

viewing, and hunting. Brown bears were hunted during both the spring (9 Apr – 15 May) and autumn (25 Oct – 15 Nov) seasons.

Six species of Pacific salmon (*Oncorhynchus* spp.) spawn in the study area, with about 3.09 million and 1.15 million individuals present during 2010 and 2011, respectively (Foster 2011; Moore 2012). Timing of salmon runs varied by species, beginning during late May and continuing through October (Foster 2011; Moore 2012). Based on abundance, the dominant ungulate was the introduced Sitka black-tail deer (*Odocoileus hemionus sitkensis*), followed by introduced mountain goats (*Oreamnos americanus*). Dominant berry species present within the study area included salmonberry (*Rubus spectabilis*) and elderberry, which produce ripe fruits between August and October. These berry species generally occurred within the alder matrix at elevations below 500 m. Other vegetation common in bear diets included nootka lupine (*Lupinus nootkatensis*), horsetails (*Equisetum* sp.), cow parsnip (*Heraculum lanatum*), *Angelica* sp., grasses, and sedges.

Bear capture & GPS collars

We captured 34 female brown bears using standard helicopter darting techniques during June 2010 and 2011 (Alaska Department of Fish & Game, IACUC Protocol No. 07-08). We immobilized bears with Telazol (1:1 mixture of tiletamine hydrochloride and zolazepam hydrochlorid; Fort Dodge Animal Health, Fort Dodge, Iowa, USA) at a concentration of 228.8 mg/ml. We fitted bears with GPS telemetry collars (Telonics Model #TGW-3790), which we programmed to obtain a GPS location every hour. Locations could be downloaded remotely during scheduled weekly intervals. We screened the GPS location data to eliminate large location errors; data screening was based on two- and three-dimensional (2D and 3D) GPS fixes in relation to the positional dilution of precision (PDOP). All 3D positions having

a PDOP >10 and 2D positions having a PDOP >5 were removed following recommendations of Lewis *et al.* (2007). The remnant GPS error was small ($\pm 10\text{m}$; *unpublished data*). An activity sensor within the GPS collars was programmed to record the proportional amount of time (seconds) that a bear's head was in the downward position (15° below horizontal) during the 5-minute period directly after the GPS location was recorded. We considered this as an index to the proportion time spent active. All GPS collars recorded locations from 15 May – 15 November, and we downloaded location data from the collars weekly from a fixed-winged aircraft. The collars were fitted with an automatic remote release mechanism scheduled to detach the collar after 2 years. The animal capture and handling protocol followed standard techniques for this species and were approved by the IACUC of the Alaska Department of Fish and Game (Protocol No. 07-08). In addition, all methods conform to the guidelines of the American Society of Mammalogists for use of wild mammals in research (Sikes & Gannon 2011).

Bed site identification

We identified the location of bed sites used by collared bears with a rule-based algorithm developed in R (R Development Core Team 2011) that was based on both location and activity data. We identified bedding sites using 2 criteria: 1) ≥ 3 inactive sequential locations, thereby ensuring a duration of >2 hours of inactivity, and 2) $\leq 20\text{m}$ between sequential inactive locations, which was equal to approximately twice the average error of the GPS collar locations. We classified locations as inactive (e.g., resting or standing) if a measurement of $\leq 15\%$ was recorded by the activity sensor (Schwartz *et al.* 2009). We used the geometric center of clusters of locations that met both of the criteria to identify putative bedding sites. To determine the accuracy and precision of the method, we visited putative

bed sites to search for evidence of recent bedding activity (e.g., excavation or depressed vegetation).

Analysis of resource selection

Because habitat selection by bears is likely scale-dependent, we examined selection of bed sites at 3 scales: home range, local, and micro-habitat scale. At the home range scale, we employed a synoptic model developed by Horne, Garton & Rachlow (2008), in which the extent of availability, $f_a(x)$, is drawn from a bivariate normal distribution of each individual's locations. At the local scale, we assumed that resources available are limited by the location of an individual prior to selecting its bed site (Arthur *et al.* 1996). Therefore, we allowed $f_a(x)$ to be dependent on the location of a bear prior to bedding and drew random locations from an empirical distribution of animal movements (Fortin *et al.* 2005). At the smallest scale, we assumed $f_a(x)$ was drawn from a local uniform distribution $\leq 100\text{m}$ from the bed site.

At each spatial scale, we quantified bear bed site selection as:

$$f_u(x, t) = \frac{f_a(x) \times w(x, t)}{\int f_a(x) \times w(x, t)} \quad , \quad (1)$$

where $f_u(x, t)$ is the probability of use at a location during time t , and $w(x, t)$ is the resource selection function describing habitat preferences at time t that transforms f_a to f_u by selectively weighting different resources (Johnson *et al.* 2008). The denominator in the equation is a normalizing constant for a weighted distribution that ensures $f_u(x, t)$ is a probability density function that integrates to 1. The resource selection function that characterizes the influence of environmental covariates on the relative use is:

$$w(x, t) = \text{Exp}[H(x)' \beta P(t)] \quad , \quad (2)$$

where $H(x)$ is a vector of covariates describing the environmental conditions at location x , β is a vector of parameters (i.e., selection coefficients) to be estimated, and $P(t)$ is an interaction term representing functions of time to allow for temporal variation in habitat selection (Ferguson, Taylor & Messier 2000; Forester, Im & Rathouz 2009).

The analysis approach was similar across all scales, in which we compared characteristics at used (bed) sites with those at available sites (Manly *et al.* 2002; Thomas & Taylor 2006). Habitat covariates were obtained either from field measurements or remotely sensed data, depending on the scale of analysis. Before modeling resource selection, we screened predictor covariates for collinearity. We assumed that if $|r| < 0.60$, then correlation between predictor covariates was not a concern (Sawyer *et al.* 2006; Ciarniello *et al.* 2007b). No covariates were considered correlated based on this criterion.

Home range: Synoptic Model

To evaluate bed site selection with the synoptic model when availability was defined as the extent of the home range, we defined $f_a(x) = BVN(\theta)$ to be a stationary (i.e., time invariant) bivariate normal distribution with parameters (θ) describing the means and variances in the x and y dimensions and the covariance (Horne, Garton & Rachlow 2008). We used a maximum likelihood approach to estimate the parameters governing the null model of home range (θ) and the selection coefficients (β) (Horne, Garton & Rachlow 2008; Johnson *et al.* 2008). The synoptic model assumes that observed locations are independent and identically distributed with respect to f_u . To reduce the potential of violating assumptions of independence, we excluded all beds sites that were initiated within 8 hours of any previously identified bed site.

To reduce computation time imposed by the large home range sizes of bears, we aggregated all raster-based covariates to a 90m² resolution. Areas mapped as water (i.e., rivers, lakes, and ocean) within the study area were considered unavailable for bedding purposes. The covariates slope, solar radiation index (SRI), hill shade, and elevation were derived from a digital elevation model (DEM) (Table 2.1). The solar radiation index was a function of slope, aspect, and latitude (Keating *et al.* 2007), and values were greatest for south-facing, moderate slopes and least for steep, northern aspects. Hill shade is a measure of solar insolation as it varies with topography and values were calculated at 1200 hrs, which was approximately the peak time for initiation of daytime beds. We aggregated a raster-based digital land cover classification provided by Kodiak Land Cover Classification (Fleming and Spencer 2007) into 2 categorical habitat types – Forest and Tall Shrub. Forest included the following cover classes: Open Birch, Closed Birch, Open Cottonwood, Dense Cottonwood, Cottonwood, Birch, and Alder. Tall Shrub included the cover classes Dense Alder, Alder-Willow Mix, Tall Willow, and Salmonberry-Elderberry. Identification and classification of anadromous streams were obtained from a database provided by the Alaska Department of Fish and Game (ADF&G *unpublished data*). We determined the distance from bedding sites to the nearest anadromous stream using the NEAR function in ArcGIS 10 (Environmental Systems Research Institute, Redlands, California).

We evaluated 3 competing hypotheses regarding bed site selection by female brown bears. The first model, Forage Availability, contained covariates that represented spatiotemporal availability of important bear foods. Based on past research (Clark 1957; Hamilton & Bunnell 1987; Barnes 1990; Hilderbrand *et al.* 1999; Fortin *et al.* 2007) and a concurrent diet analysis (Sorum 2013; Ch. 1), we identified 3 general food categories

important to brown bear diets within our study area: 1) new growth from forbs and graminoids, 2) salmon, and 3) berries and roots, and we modeled the spatio-temporal distribution of each category. Throughout the spring and summer months, new growth of vegetation constitutes a large proportion of the diet, but the general distribution of this food item changes through time. During the spring, we included the covariates SRI and elevation, and we expected selection for lower elevation areas with higher SRI values (Table 2.2). Therefore, we included an interaction term P_{spring} for these covariates which equaled 1 if time-of-year was 1 June – 24 June and 0 if otherwise. During the summer, delayed plant emergence and rapid rates of plant growth have been suggested to influence space use by brown bears (Atwell *et al.* 1980), and these conditions are promoted at higher elevation alpine sites (Körner 1989; Fox 1991). Therefore, we included an interaction term P_{summer} for this covariate, which equaled 1 if time-of-year was 25 June – 15 August and 0 if otherwise. Salmon were identified in the diet of bears during both the early and late salmon runs, and they occurred in greater proportions during the late run. Therefore, we expected selection for areas closer to streams during both periods, but that the effect would be strongest during the late run. To examine this relationship, we included the interaction terms $P_{salmon.early}$ and $P_{salmon.late}$ for this covariate, which equaled 1 if time-of-year was 1 July–15 August or 16 August–15 October, respectively, and 0 if otherwise. Early in the autumn (15 August – 1 October), fruit from important berry-producing shrubs (i.e., salmonberry and elderberry) appeared in the diet of bears. After 1 October, northern groundcone (*Boschniakia rossica*), a forage root, also began appearing in the diet of bears (Sorum 2013; Ch. 1). We included the covariate *berry.root*, a habitat type that represents spatial distribution of forage berries and northern groundcone, and expected selection for *berry.root* during both periods, but that the

effect of selection to be strongest during the later season when these food items more prevalent in the diet of bears (Sorum; Ch.1). To examine this relationship, we included the interaction terms $P_{fall.early}$ and $P_{fall.late}$ for this covariate, which equaled 1 if time-of-year was 15 August–1 October or 1 October–15 October, respectively, and 0 if otherwise (Table 2.2).

Our second model, the Thermal Regulation Hypothesis, suggested that bears select habitats for bedding that reduce amount of direct sunlight. We included the covariates hill shade and habitat types that would provide relatively more canopy cover, forest and tall shrub (Table 2.1). We predicted an avoidance of hill shade, indicating selection for cooler north-easterly facing slopes, and selection for forest and tall shrub habitat types. During nocturnal time periods (2300-0500 hrs), we assumed bed site selection would not be influenced by these covariates due to the absence of solar radiation. To examine this relationship, we included interaction term P_{day} (equaled 1 if time-of-day was 0600-2200hrs and 0 otherwise) so we could quantify day selection (Table 2.2). Additionally, in higher latitude environments, such as our study site, the amount and intensity of solar radiation at a specified location changes considerably throughout the year. To account for this change, we allowed the value of hill shade to change over time. Hill shade values were calculated on 15 June, 15 August, and 1 October, which represented periods 1 June – 14 July, 15 July – 14 September, and 15 September – 15 October, respectively.

Mysterud (1983) reported that at bed sites, bears used steeper slopes and combinations of vegetative and topographical features that increased concealment suggesting that bears used these features to improve their safety. Thus, the final model, Conspecific Avoidance, contained covariates for slope and tall shrub (Table 2.1). We predicted that steeper slopes combined with a matrix of dense vegetation found in the tall shrub habitat type made access

to a bed site by conspecifics more difficult and increased the ability of a bear using the bed site to detect approaching conspecifics. Unlike the Thermal Regulation model, here we predicted selection for tall shrub during both diurnal and nocturnal periods. To examine this relationship, we included an interaction terms P_{day} and P_{night} (equaled 1 if time-of-day was 2300-0500hrs and 0 otherwise), so we could quantify both day and night selection (Table 2.2).

Local: Step selection function

For this scale of analysis, we considered that resources available to an animal at time y are dependent on the location of the animal at $y-1$. Therefore, we compared bed sites at time y to random sites associated with a location created 2 hours prior, $y-1$ (Arthur *et al.* 1996). We used a conditional logistic regression model and paired each bed site to 30 random locations (Compton, Rhymer & McCollough 2002; Ciarniello *et al.* 2007b). We used an empirical distribution of animal movements collected from collared bears to select the random sites. From vectors of 3 animal locations in which the identified bed site was the final location, we sampled step length and turning angles (Fortin *et al.* 2005; Forester, Im & Rathouz 2009). Hence, we used movements associated with bedding activities to define availability. Step length was determined by the straight-line distance between animal locations and turning-angles characterized as the angle from the previous step to the next. The same covariates were included in the models that were developed for the analysis at the home range scale, but the resolution of the raster-based covariates was reduced to 30 m because we were evaluating habitat selection at a finer-scale over a smaller extent. We used an information theoretic approach to evaluate the strength of evidence for alternate hypotheses at the local scale (Table 2.2).

Micro-habitat: Uniform buffer

In this design, we explored what factors influence bed site selection at a micro-scale by evaluating the area immediately surrounding the bed sites that we ground-truthed by field investigations and comparing the habitat features to what was available within 100 m. During June 2011, we randomly selected 8 collared bears for which to quantify bed site selection at the micro-habitat scale by visiting their putative bed sites during most of the active season (6 June – 15 Oct). If a GPS collar malfunctioned (i.e., no or limited location data were collected) or prematurely deployed (i.e., bear died or slipped the collar), then we randomly selected another collared bear so that we continued to collect micro-habitat data on no fewer than 6 bears. For each individual, we selected a putative bed site every 2 days for field visitation and habitat characterization, and available sites were randomly assigned 40-100m away from the used bed site.

At each putative bed site, we searched for evidence of bedding (e.g., excavation, depressed vegetation) within a 20-m radius surrounding the central GPS location, and we measured habitat features at bed sites that were potentially important for foraging, thermal regulation, and conspecific avoidance (Table 2.3). We established 2 40-m transects that were perpendicular to each other and centered on the actual bed. The direction for the first transect was randomly selected. At each randomly selected available site, the transects were centered on the GPS location. We used the point-intercept method and a sighting device to estimate percent cover by species. Sampling points were at the bed and at 2-meter intervals along each transect, for a total of 41 intercepts per site. Readings were made from 1.5 meters above ground level, looking downward to characterize understory vegetation and upward to estimate overstory cover. We consider 5 forb species as important forage for bears: *Angelica*

genuflexa, *A. lucida*, *Heraculum lanatum*, *Urtica lyallii*, and *Lupinus nootkatensis*. We consider 2 berry-producing shrubs as important forage species, elderberry and salmonberry (*Rubus spectabilis*), and we also estimated cover of sedges (*Carex spp.*) in the understory. We estimated density of stems by counting all stems >2.5 cm in diameter that crossed the transect in the understory (<1.5m height). We categorized the micro-topography at each bed and random site as: cliff, rock-outcropping, ridgeline, or none. Distance to nearest stream with salmon was determined using a GIS as in the home range and local scale analyses.

Using the empirical data collected for each bed site, we included covariates that could influence bed site selection at a micro-habitat scale. Similar to the broader scales of analysis, the Forage Availability model contained covariates that measured the availability of food items considered important to the diet of brown bears, including distance to nearest anadromous stream, and cover of forbs, sedges, and berry-producing shrubs (Table 2.3). We interacted each covariate with the appropriate time indicator variable to estimate change in availability of the forage throughout the season (Table 2.2). The second model, Thermal Regulation, contained one variable associated with favorable microclimate conditions for thermoregulation by brown bears (i.e., canopy closure), and we predicted that daytime bed sites would have more canopy closure (Moe *et al.* 2007). We included the covariate canopy and the interaction term P_{day} , which assumed neither selection nor avoidance of canopy closure at bed sites that were initiated at night. Finally, the Conspecific Avoidance model contained the covariates stem density, elderberry cover, and micro-topography category. Based on previous field investigations and literature (Mysterud 1983), we predicted that bears would select features that reduced access to bed sites by conspecifics and increased the ability of a bear using the bed site to detect approaching conspecifics. Therefore, we

predicted that stem count and elderberry cover would be greater, and features categorized as having micro-topography would occur more often at used bed sites compared to available sites (Table 2.2).

Model Selection

We used an information theoretic approach to evaluate strength of evidence for alternate hypotheses explaining bed site selection (Burnham & Anderson 2002; Horne, Garton & Rachlow 2008). Our candidate model set included a null model (no habitat covariates) and the competing 3 models that reflected our hypotheses about behavior of bears. We selected the best model within the competing model set using Akaike's Information Criteria corrected for small sample sizes (AIC_c), we ranked candidate models using the difference in AIC_c values from the model with the smallest value (ΔAIC_c), and we determined the relative likelihood of a model using Akaike weights (Burnham & Anderson 2002).

For population-level inference of habitat selection, we averaged parameter estimates ($\hat{\beta}$) across individuals. For a conservative measure of precision, we considered a coefficient to be significant if 2 times the standard error of the mean did not contain zero (Boyce 2006; Fieberg *et al.* 2010). Treating each individual as the sampling unit allowed us to examine potential intraspecific variation in bedding behaviors (Thomas & Taylor 2006), while also maintaining inferences at the population-level (Marzluff *et al.* 2004; Sawyer *et al.* 2006).

RESULTS

Bed site identification

The rule-based clustering algorithm accurately identified the location of the bedding sites used by the collared brown bears. We visited 375 putative bed sites from 12 individuals

(mean bed/bear = 31.3, SE = 4.8). On average, we visited bedding sites 14 days (SE = 0.5) after they were used by the bear. If beds were present, we usually found them quickly, in many cases before we implemented the systematic search procedure. We found evidence of recent bedding activity at 97.3% ($n = 365$) of the putative bedding sites that we visited. Evidence of bedding was, on average, 6.7 m (SE = 0.4) from the predicted bedding site.

Applying the criteria for distinguishing bed sites to our entire data set, we identified 3,943 unique bed sites from 30 individuals over 2 years (June 2010 – June 2012). Twenty-one collared bears were monitored for one year and 9 collared bears were monitored for 2 years. On average, there were 0.88 days (the interquartile range 0.45 – 1.42 days) between successive bed site identification for each individual. After excluding bed sites within 8 hours of a previously identified bed site and those with a land classification of water ($n = 61$), we included 3,422 separate bed sites in the analyses at the home range and local scales.

The timing of bed site initiation was not regularly distributed throughout a day. There was a bimodal peak, with the greater of the two peaks occurring around midnight and the lesser occurring around noon. Even though the nocturnal period was, on average, 1/3 the duration of the diurnal period, the proportion of beds identified at night compared to the day (0600-2300hrs) was nearly equal (night 48%; day 52%; Fig 2.2).

Home range: Synoptic Model

Thirty collared bears had a sufficient number of bed sites (>18) to analyze habitat selection at the home range scale. Of these, the average number of bed sites identified over the entire study period per bear was 114 (range 33 – 285). Model importance, as measured by the percent of individuals for which each model was within the top model set (<2 AICc),

in descending order was Forage Availability, Thermal Regulation, Conspecific Avoidance, and Null (Table 2.4).

At the home range scale, the Forage Availability model was the most parsimonious for 27 of the 30 collared bears (90%), suggesting that availability of food resources was an important driver of bed site selection at the population level. Furthermore, the Forage Availability model received on average >99% of the AICc weight when it was the top model, suggesting strong model performance (Table 2.4). Five of the 7 covariates were significant across the population, and the direction of the effects also supported our expectations that forage availability was the most important factor influencing selection of bed sites at the scale of the home range. Average probability ratios indicated that during the spring when snow covered vegetation at moderate to high elevations, every 100m increase in elevation resulted in a decrease in selection by approximately $\frac{1}{4}$ and bears were approximately 1.4 times more likely to select bed sites for every 10% increase in solar radiation; these results support the conclusion that bears selected areas with features that promoted snowmelt and advanced plant phenology during spring (Table 2.5).

At the home range scale, bears also bedded closer to salmon streams and berries when these forage resources were available. During the early and late salmon runs, average probability ratios indicated that every 100 m of additional distance from streams resulted in a 14% and 22% decrease in selection, respectively (Table 2.5). After 1 October, bears were 1.24 times as likely to select bed sites in habitat types associated with berries and northern groundcone (*berry.root*) compared to other habitats. Interestingly, this same strength of selection for berries was not detected before 1 October, when bed sites were only 0.32 times as likely to be in the *berry.root* habitat.

The Thermal Regulation model for selection of bed sites was poorly supported by our data at the home range scale, receiving the most support from only 2 individuals (7%). For significant covariates, average probability ratios indicated that during the day, bears were about 2.4 and 1.6 times more likely to bed in forest and tall shrub habitat types, respectively, compared to other habitats (Table 2.5). The Conspecific Avoidance model received most support from only 1 individual (3%), the direction of slope was opposite of what we predicted, and tall shrub was selected during the day, but not at night across all bears.

Local: Step selection function

Thirty individuals had a sufficient number of beds to analyze habitat selection at the local scale. Of these, the average number of bed sites per individual was 96 (range 29 – 266). In contrast to the home range scale, our models did not appear to characterize selection of bed sites at the local scale. The rankings of competing models, in descending order, was Null, Conspecific Avoidance, Thermal Regulation, and Forage Availability (Table 2.4).

At the local scale, the Null model received the most support for 14 of the 30 individuals (47%) suggesting that our predictor variables did not represent selection of bed sites at this scale. The Thermal Regulation model received the most support for 6 individual (20%). Average probability ratios indicated that bears were approximately twice as likely to bed in the tall shrub habitat type compared to other habitats. The Forage Availability model was the most parsimonious model for 5 individuals (17%). For significant covariates, average probability ratios indicated that during the spring, every 100m of additional elevation resulted in a decrease in selection by about $\frac{1}{3}$, and during the late salmon run, every 100m of additional distance from streams decreased selection by about $\frac{3}{4}$. The Conspecific Avoidance model also was the most parsimonious for 5 individuals (17%). Average

probability ratios indicated that bears were approximately 1.9 times as likely to bed in tall shrub habitat during the day compared to other habitats. Overall, local models exhibited inconsistent results, high model uncertainty, and consequently, a general lack of consistent selection at this scale (Table 2.5).

Micro-site: Uniform buffer

Ten collared bears had a sufficient number of bed sites to analyze habitat selection at the micro-habitat scale. Of these, the average number of bed sites per bear was 33 per year (range 19 – 48). Similar to the home range scale, our models appeared to characterize bed site selection, however, they also revealed variation among individuals in the factors shaping selection. Model importance at the population level in descending order was Conspecific Avoidance, Thermal Regulation, Forage Availability, and Null (Table 2.4).

For the micro-habitat scale, the Conspecific Avoidance model was most parsimonious for 4 individuals (40%). Average probability ratios indicated that bears were approximately 1.5 and 1.2 times more likely to bed at sites with a 10% increase in stem count and elderberry cover, respectively, and about 37 million times more likely to bed at sites classified as having micro-topography (i.e., cliffs, rock-outcroppings or ridges) compared to areas that did not. Similarly, the Thermal Regulation model received the most support for 4 (40%) of the 10 individuals. Average probability ratios indicated that bears were 2.5 times more likely to select a bed with every 10% increase in canopy closure. The Forage Availability model was the most parsimonious for only one individual, and none of the covariates were significant across animals, suggesting that the distribution of food items had little influence on the selection of bed sites by brown bears at a micro-habitat scale. The Null model also received the most support for one individual (Table 2.5).

DISCUSSION

We demonstrated that factors influencing bed site selection by female brown bears are strongly scale dependent in ways that allow females to simultaneously fulfill multiple life-history requirements (i.e., shelter, security, and food). As expected (H1), females selected bedding locations that enhanced their ability to acquire food at the broadest scale and reduced their exposure to risk of conspecific aggression and thermal stress at the finest scale. Our results support the hypothesis that animals select habitat that provides their most important limiting resources at larger spatial scales, while meeting secondary needs at finer scales (Rettie & Messier 2000). The importance of forage in shaping habitat use at large spatial scales is consistent with expectations for brown bear populations in relatively unaltered ecosystems like our study site (McLoughlin *et al.* 2002; Milakovic *et al.* 2012).

We accurately identified bed sites from GPS locations of bears using both movement and activity data to develop a rule-based clustering algorithm. In fact, 97% of the putative bedding locations that we visited ($n = 375$) had evidence of recent bedding <7 m from the predicted location. These results demonstrated that the criteria we developed were reliable predictors of the location of bed sites used by female brown bears. Other studies identifying important areas used by animals, such as kill sites by wolves (Webb, Hebblewhite & Merrill 2008) or cougars (Knopff *et al.* 2009), have advocated clustering methods and have reported high success rates, as well. Linking animal locations with specific behaviors improves our ability to make inferences about the underlining mechanisms that govern animal movements and distributions (Beyer *et al.* 2010), and in our study, allowed us to isolate resources used during bedding from those used during other behaviors.

Perhaps counter intuitively, food availability appeared to be the most important factor affecting selection of bedding sites by bears within home ranges across the population. This result makes sense, however, in the context of the ecology of this species; brown bears are large-bodied omnivores that forage extensively to meet their energetic requirements (Hilderbrand *et al.* 1999; Robbins *et al.* 2007; Van Daele *et al.* 2013). By positioning resting sites in areas that improve access to seasonally abundant food resources (e.g., near streams with salmon), bears can minimize travel time between foraging and bedding locations. By selecting habitat to obtain forage at larger scales, bears were able to address other important needs (thermoregulation and security) at finer scales.

Temperature is considered a crucial abiotic factor directly influencing patterns of animal space use (Hansen *et al.* 2011). Selection patterns of bed sites by brown bears appeared to be influenced by factors that reduced exposure to solar radiation across multiple scales; however, only at the micro-site scale was thermal regulation the most influential mechanism. At the population level, areas that had higher proportions of canopy cover were selected. Other studies investigating patterns of habitat selection also have reported fine-scale responses to temperature by large mammals (Bowyer & Kie 2009; Leblond, Dussault & Ouellet 2010; van Beest, Van Moorter & Milner 2012). Quantifying such thermoregulatory behavior is a necessary first step to effectively evaluate climate-induced effects on population dynamics of animals (Grosbois *et al.* 2008).

Although our sample of collared bears only included 4 females with cubs, our results suggested that the mechanisms influencing space use by these maternal females differed from lone females. As expected at the micro-site scale, females with cubs selected habitat features that enhanced security by bedding in areas with thicker vegetation and micro-topographic

features. We often observed bed sites used by females with cubs in extremely dense vegetative cover and/or near edges of cliffs or on rock outcroppings >3m high, a trend that was less evident for solitary females. Risk of infanticide by other bears strongly affects behavior of females with young cubs (Dahle & Swenson 2003; Ben-David, Titus & Beier 2004; Rode, Farley & Robbins 2006a; Martin *et al.* 2012), and it appeared to influence patterns of bed site selection by maternal females in our study. Like non-maternal females, however, availability of food was the most important factor influencing habitat selection at the broadest scale. This result is perhaps not surprising considering the high nutritional requirements imposed by reproduction and lactation (Farley & Robbins 1995; Hilderbrand *et al.* 2000). The strategy of obtaining forage at broad scales while seeking security at specific bedding sites likely allowed maternal females to meet these potentially conflicting needs simultaneously.

Top-down factors likely influence patterns of space use for many brown bear populations (Ciarniello *et al.* 2007a; Nielsen *et al.* 2010), yet little research has addressed how bears select resources to reduce exposure to such risks at finer spatial scales. Within an area readily accessible to an individual (i.e., micro-site scale), we demonstrated that features that could simultaneously impede access and enhance early detection of other bears were important factors explaining patterns of bed site selection by females with cubs. However, at broader scales, the risk of mortality did not appear to influence bed site selection by females, even those accompanied by cubs. It is likely, however, that maternal females used other habitat features not included in the Conspecific Avoidance model at the broader scales to reduce the risk of aggressive encounters. Females might avoid areas used by adult males (Dahle & Swenson 2003; Ben-David, Titus & Beier 2004; Rode, Farley & Robbins 2006a;

Suring *et al.* 2006), but we did not have data on male distributions in our study area to investigate spatial relationships between the sexes. However, we did observe differential space use between lone females and those with cubs. During spring when mating occurs, maternal females selected for higher elevation areas, which likely have less forage available, but might allow females to spatially segregate from lower elevation areas frequented by males. In addition, females with cubs exhibited a weaker selection for streams with salmon, suggesting that they bedded further from streams than lone females.

Although it is unlikely that we identified all bedding sites for collared bears, we were able to identify many for each individual, and we do not believe that unidentified sites biased our analyses of habitat selection during bedding. Particularly for resting bears, body position and posture can reduce success of GPS location acquisition, presumably because orientation of the antennae and location of the collar shift during bedding (Graves & Radandt 2004; D'Eon & Delparte 2005; Graves & Waller 2006). Likewise, Schwartz *et al.* (2009) reported that fewer successful GPS locations were recorded when bears were likely resting and that fix success was invariant to most vegetation and terrain factors, with the exception of north facing slopes with heavy conifer cover. Prior to deployment, we conducted an informal accuracy assessment using the GPS collars, and neither fix success nor location accuracy was affected by land cover or terrain (*unpublished data*). Therefore, unidentified bed sites in our study were likely a function of animal behavior rather than habitat.

At the intermediate scale of our analyses (i.e., the local scale), we were unable to detect consistent patterns of bed site selection by brown bears. This might occur for several reasons, some of which might be related to how we selected the scales and characterized the habitat rather than the behavior of the animals (Hobbs 2003). For example, we might not

have included habitat variables that strongly influence selection at this scale, or the resolution of our assessment of resource use and availability might have been incorrect and mismatched. Yet, we were able to detect strong patterns of selection for bed sites at both larger and smaller spatial scales, which provided insight into how animals meet diverse needs simultaneously.

Patterns of space use by animals are complex and driven by varying life-history objectives, yet remotely-sensed locations rarely provides information about what the animal is doing (Kertson & Marzluff 2010). By increasing the behavioral resolution of the animal location data, we were able to gain insight into the underling mechanisms that govern selection of bed sites. Furthermore, using a multi-scale analysis facilitated investigation of how animals meet multiple resource needs concurrently, and this approach informed our understanding about which factors might be most limiting to population fitness (Rettie & Messier 2000; Boyce 2006). Brown bears, in particular, cover large areas, forage on diverse foods that vary in availability through time and space, and in high-density populations like Kodiak, require habitat features that provide both shelter and security cover. Long-term conservation of bears and other large-bodied animals will require conservation of habitat that allows them to meet diverse resource needs at appropriate scales.

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Table 2.1. Description of spatial ($H(x)$) and temporal ($P(x)$) model parameters and specific covariates in each models evaluating habitat selection by bedded female brown bears in southwestern Kodiak Island, Alaska, USA.

Model Parameters	Specific Covariates	Description	
$H(x)$	SRI	Solar radiation index as a function of slope, aspect, and latitude (Keating et al. 2007)	
	elev	Elevation at identified point	
	dist.stream	Distance (m) to active salmon stream	
	berry.root	Land cover map depicting the distribution of important berries and roots	
	hill.shade	Combination of slope and aspect to measure solar insolation as it varies with topography (provide azimuth and sun angle, and/or dates) (negative coefficient indicate selection for cooler, northeast aspects, while positive coefficients indicate selection for warmer southwest aspects)	
	forest	Birch & cottonwood forest with canopy closure > 10%	
	tall.shrub	Alder & willow complex with canopy closure > 10%	
	slope	The slope ($^{\circ}$) at the identified point	
	$P(t)$	spring	1 June - 24 June
		summer	25 June - 14 August
fall.early		15 August - 31 September	
fall.late		1 October - 15 October	
salmon.early		1 July - 14 August	
salmon.late		15 August - 15 October	
day		0600 – 2200hrs	
night		2300 – 0500hrs	

Table 2.2. Description and expected direction of *a priori* candidate models used to evaluate multi-scale selection of bed sites by brown bears in southwest Kodiak Island, Alaska, USA.

Model	Working Hypothesis	Scale	Model Structure	Expected Results
1 Forage Availability	Distribution of food items influences bed site selection.	HR,	$(\beta_1 \times P_{\text{spring}}) \text{SRI} +$	$\beta_1 > 0, \beta_2 < 0,$ $\beta_3 > 0, \beta_4 < 0$
		Mid	$(\beta_2 \times P_{\text{spring}}) \text{elev} +$ $(\beta_3 \times P_{\text{summer}}) \text{elev} +$ $(\beta_4 \times P_{\text{salmon.early}}) \text{dist.stream} +$ $(\beta_5 \times P_{\text{salmon.late}}) \text{dist.stream} +$ $(\beta_6 \times P_{\text{fall.early}}) \text{berry.root} +$ $(\beta_7 \times P_{\text{fall.late}}) \text{berry.root}$	
		Micro	$(\beta_1 \times P_{\text{spring\&summer}}) \text{forb.cov} +$ $(\beta_2 \times P_{\text{spring\&summer}}) \text{sedge.cov} +$ $(\beta_3 \times P_{\text{fall}}) \text{berry.cov} +$ $(\beta_4 \times P_{\text{salmon}}) \text{dist.stream}$	$\beta_1 > 0, \beta_2 > 0,$ $\beta_3 > 0, \beta_4 < 0$
2 Thermal Regulation	Thermal regulation influences bed site selection	HR,	$(\beta_1 \times P_{\text{day}}) \text{hill.shade} +$	$\beta_1 < 0, \beta_2 > 0,$ $\beta_3 > 0$
		Mid	$(\beta_2 \times P_{\text{day}}) \text{forest} +$ $(\beta_3 \times P_{\text{day}}) \text{tall.shrub} +$	
		Micro	$(\beta_1 \times P_{\text{day}}) \text{canopy}$	$\beta_1 > 0$
3 Conspecific Avoidance	Bed sites are associated with habitats that improve concealment and avoidance from conspecifics	HR,	$\beta_1(\text{slope}) +$	$\beta_1 > 0, \beta_2 > 0,$ $\beta_3 > 0$
		Mid	$(\beta_2 \times P_{\text{day}}) \text{tall.shrub} +$ $(\beta_3 \times P_{\text{night}}) \text{tall.shrub}$	
		Micro	$\beta_1(\text{stem}) +$ $\beta_2(\text{elderberry.cov}) +$ $\beta_3(\text{micro.topo})$	$\beta_1 > 0, \beta_2 > 0,$ $\beta_3 > 0$

Table 2.3. Description and period each covariate was considered available at a fine scale in models comparing female brown bear bed sites with available in southwester Kodiak Island, Alaska, USA.

Model Parameters	Specific Covariates	Description
$H(x)$	forb.cov	The proportion of forbs at identified location determined at 41 point-intercepts
	sedge.cov	The proportion of <i>Carex spp.</i> at identified location determined at 41 point-intercepts
	berry.cov	The proportion of berry-producing shrubs at identified location determined at 41 point-intercepts
	dist.stream	Distance (m) to active salmon stream
	canopy.cov	Proportion of canopy closure, above 1.5m above the ground, at identified location determined at 41 point-intercepts
	stem count	The number of stems > 1in diameter that crossed the transect below 1.5m height
	elderberry.cov	The proportion of elderberry below 1.5m height determined at 41 point-intercepts
	micro.topo	Presence or absence of micro-topography features (i.e., cliff, rock-outcropping, ridgeline) at identified location
$P(t)$	spring&summer	1 June – 14 August
	fall	15 August – 15 October
	salmon	1 July – 15 October
	day	0600 – 2200hrs

Table 2.4. Model selection results for 3 scales of analysis reporting the number of individuals for which each model of bed site selection received the most support. Average and range of Akaike weights and percent of times that each model occurred in the top model set ($< 2\text{AICc}$ of the top model) are reported for models of bed site selection by brown bears on Kodiak Island, Alaska, USA.

Hypothesis	Home Range Scale				Local Scale			Micro-Site Scale				
	No. bears	Akaike wt		% $<2\text{AICc}$	No. bears	Akaike wt		% $<2\text{AICc}$	No. bears	Akaike wt		% $<2\text{AICc}$
		Avg	Range			Avg	Range			Avg	Range	
1. Null	0			0	14	0.66	0.44-0.89	63	1	0.34		20
2. Forage	27	0.99	0.85-1.00	93	5	0.84	0.54-0.99	23	1	0.46		30
3. Thermal	2	0.67	0.48-0.86	7	6	0.67	0.46-0.87	27	4	0.76	0.41-0.99	60
4. Safe	1	0.99		3	5	0.67	0.46-0.96	37	4	0.75	0.43-1.00	70

Table 2.5. Average parameter estimates and probability ratios across home range, local, and micro-habitat scales used to characterize selection of bed sites by female brown bears on Kodiak Island, Alaska, USA.

Hypothesis	Covariates	Home range		Local		Covariates	Micro-Site	
		β	Prob Ratio	β	Prob Ratio		β	Prob Ratio
Forage Availability								
	P_{spring} x SRI ^a	3.1	1.36	0.5	1.05	$P_{spring\&summer}$ x forb.cov ^a	-0.6	0.94
	P_{spring} x elev ^b	-3.8	0.74	-4.1	0.66	$P_{spring\&summer}$ x sedge.cov ^a	-67.5	<0.01
	P_{summer} x elev ^b	-5.5	0.64	-0.8	0.92	$P_{spring\&summer}$ x dist.stream ^a	-15.5	0.08
	$P_{salmon.early}$ x dist.stream ^b	-17.2	0.86	-5.9	0.45	$P_{spring\&summer}$ x berry.cov ^a	0.2	1.02
	$P_{salmon.late}$ x dist.stream ^b	-28.4	0.78	-10.5	0.24			
	$P_{fall.early}$ x berry.root ^c	-1.2	0.32	-1.1	0.32			
	$P_{fall.late}$ x berry.root ^c	0.2	1.24	0.1	1.15			
Thermal Regulation								
	P_{day} x hill.shade ^a	0.3	1.03	0.8	1.08	P_{day} x canopy.cov ^a	9.2	2.5
	P_{day} x forest ^c	0.9	2.44	-0.4	0.64			
	P_{day} x tall.shrub ^c	0.5	1.59	0.6	1.89			
Conspecific Avoidance								
	slope ^a	-2.3	0.10	1.2	3.23	stem ^a	4.4	1.56
	P_{day} x tall.shrub ^c	0.5	1.59	0.6	1.89	elderberry.cov ^a	1.8	1.20
	P_{night} x tall.shrub ^c	-0.1	0.88	-0.7	0.49	micro.topo ^c	17.3	37,132,382

^a - Probability ratios represent the proportional change in the utilization distribution for every 10% increase.

^b - Probability ratios represent the proportional change in the utilization distribution for every increase in 100m.

^c - Probability ratios represent how much less or more likely that a bear will bed in a category compared to another category.

Note: Bold values indicate significance at the population level.

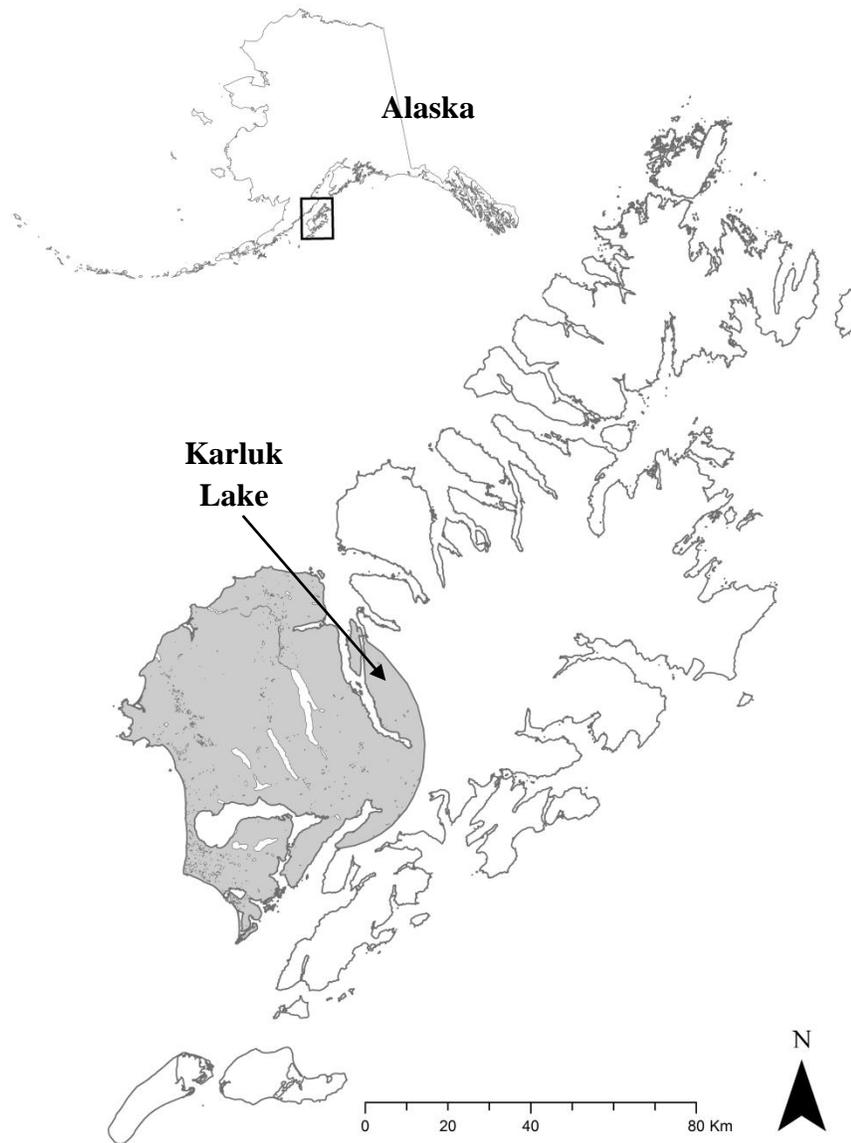


Figure 2.1. The study area (gray) encompassing southwestern Kodiak Island, Alaska, which is set within the Gulf of Alaska, USA.

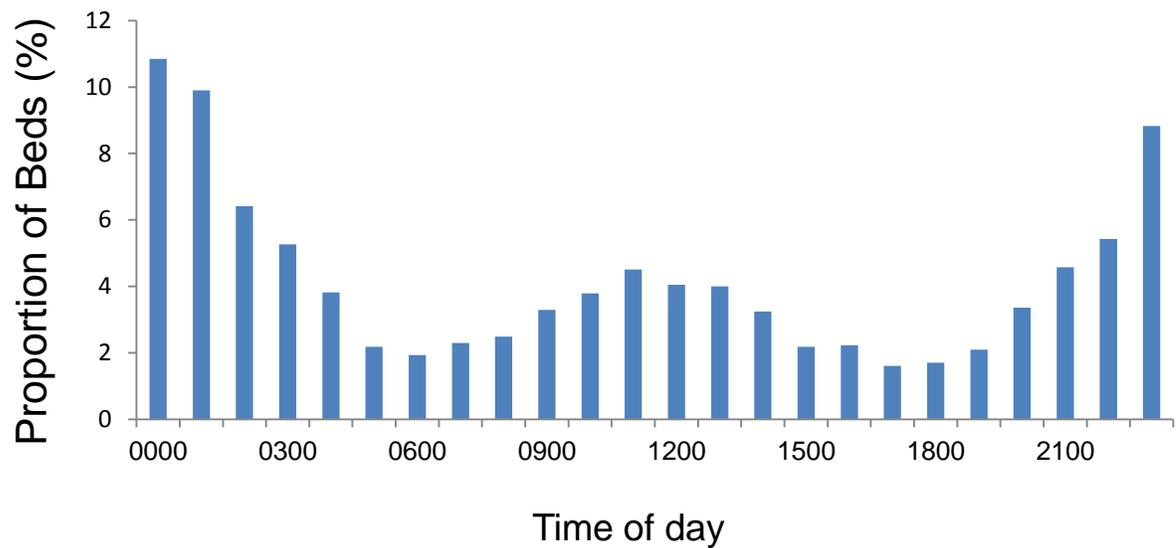


Figure 2.2. The number of bed sites that were initiated by female brown bears on Kodiak Island, Alaska, USA, during each hour of the day from June 1st to October 15th during 2010-2011.

CHAPTER THREE:

Salmon Abundance and Timing: Protocol Development

SUMMARY

1. Salmon are an important food source for coastal populations of brown bears, and consequently, their movement patterns likely influence patterns of space use by bears. Understanding variation in temporal availability and abundance of salmon could improve managers' ability to evaluate and predict how changes in salmon distribution and abundance might alter brown bear population dynamics and movements.
2. We used an autonomous video system to enumerate salmon escapement within tributaries of Karluk Lake, Alaska. We counted both the upstream and downstream movements over a 24-hour period for 10 days on Meadow Creek and 12 days on Canyon Creek.
3. In general, salmon appeared to move upstream during the daytime at an average rate of 1.3 fish/hr and downstream at an average rate -11.0 fish/hr during nocturnal periods. Future studies investigating salmon movements and abundance should consider variability throughout the day, as well as the seasons.

INTRODUCTION

Salmon are an important food source for brown bears, and they are especially important for females because body mass, reproduction, and population density are positively influenced by the amount of meat in their diet (Jacoby *et al.* 1999; Hilderbrand *et al.* 1999). What remains unknown is how the spatial and temporal variability in

salmon resources affects movements and space use by bears. An understanding of this relationship would provide a foundation for evaluating the implications of future changes in salmon distribution and abundance on brown bear populations.

Recent analysis of nitrogen isotopes using sediment cores from Karluk Lake suggested large fluctuations in salmon abundance during the last 500 years, including an unprecedented decrease within the past 100 years (Finney 1998). The decrease suggested by Finney (1998) was corroborated by recent studies based on weir-escapement data that also documented an overall decline in adult salmon production since 1922 (Barnaby 1944; Koenings & Burkett 1987; Schmidt *et al.* 1997). The individual and population-level responses of bears to these long-term changes are unknown. Although retrospective analyses on bear behavior and productivity are not feasible, it is possible to assess how bears respond to shorter-term spatial and temporal variation in abundance of salmon within Karluk Lake tributaries. Because bears are long-lived and behaviorally adaptable, they adjust patterns of space and resource use in response to fine-scale variation in resource availability. An understanding of this process is important for adjusting current management practices, and for developing hypotheses about potential long-term effects of changes in availability of critical resources.

Recent advances in GPS telemetry have enhanced the ability to investigate habitat use of brown bears at finer spatiotemporal resolutions. These advances in our ability to monitor movement patterns when coupled with well-established analytical tools can help us explain or predict the relative probability of use across a landscape based on the spatial and temporal arrangement of resources. To accomplish this, a monitoring system is needed to gather information on timing, abundance, and availability to bears of spawning

salmon entering Karluk Lake. Our objective was to develop and test a pilot protocol for quantifying salmon escapement on Karluk Lake tributaries. The aim was to develop a system that can be used more widely for long-term monitoring of stream-spawning salmon in the Karluk drainage.

We considered several potential methods for quantifying timing and abundance of salmon runs; weir, sonar, and hydroacoustic methods were dismissed because of associated high cost. Aerial surveys seemed plausible because flights for counting bears already are conducted along the same streams, but this method can be highly variable and provides only an index of relative abundances (Baron 1984). Tower surveys could provide sufficient accuracy, but these methods are labor-intensive and cost-prohibitive for monitoring multiple stations. A retrospective sampling strategy using video cameras provides accuracy equal to weir-based methods while maintaining relatively low labor requirements (Davies, Kehler & Meade 2007; Otis *unpublished data*). This strategy would allow us to attain an estimate of salmon abundance without the biases associated with *in situ* observations because salmon do not exhibit avoidance of cameras (Shardlow 2001). In addition, variability in observer experience can be more easily tested when cameras are used to record fish passage (Shardlow 2001). Other benefits to photo-enumeration are that it is less expensive and safer than aerial, foot, or tower surveys, and it reduces the potential for bear-human confrontation because it can enumerate spawning salmon for many days without human presence. Additionally, digital videos can be reviewed many times without degrading, are easily archived, and represent a permanent record that can be used at future times (Edwards 2005).

METHODS

We video recorded the salmon entering Canyon Creek (CC), Meadow (MC), and O'Malley Creek (OC) throughout the summer (10 July – 18 Sept.) by mounting video camera systems near the mouths of the streams (10-75m upstream; Fig. 3.1). Due to the shallow depths of the tributaries entering Karluk Lake, we assumed that all fish are available to be counted once they enter the stream (Fortin *et al.* 2007). In an attempt to minimize two-directional fish movements within the field of view of the camera, we identified areas in the stream where fish tend not to congregate or hold, but rather move rapidly upstream.

Video Monitoring Setup

We used high resolution, low-lux capacity black and white video cameras with a 2-12mm vari-focal, auto-iris lens. A circular polarizing filter was affixed to the camera lens reducing surface glare, and the camera was protected inside weather proof camera housing. Images were recorded on a digital video recorder (DVR) at 5 frames/sec to optimize storage space without degrading the ability of viewers to count fish passing the video site. The DVR recorded all video onto a 32GB SD memory card, which provided approximately 2.8 days of continuous 24-hr recording. The DVR, batteries, and additional sensitive materials were stored in an aluminum bear-proof box.

The width of the stream and subsequently the field of view (FOV) of the camera was 6m, 8m, 10m at MC, CC, and OC, respectively. Cameras were attached to a tri-pod and placed above the stream at a height of approximately 6 m (Fig. 3.1). Stream site locations were selected that have few riffles and provides a clear view of the bottom. The

camera lens was pointed as close to directional north as possible to reduce glare from the water surface.

To provide a visual contrast we used 3 mm polyethylene white panels to aid the ability of the camera to capture fish movements (Fig. 3.1). The upstream edges of the panels were secured to a steel chain, which was secured to the bottom of the stream by rebar. Panels were connected to the chain and each other with zip ties. To improve our ability to detect nocturnal movements we fastened LED lights encapsulated in clear vinyl tubing to the substrate panel. LED lights were only used during nocturnal hours and set on a timer. This provided enough lighted contrast for the video camera to record any/all salmon movements. Electronic components were powered by two 12VDC deep cycle battery. Two 50 Watt solar panels were used to recharge the battery. A charge control regulator was used to avoid overcharging batteries. Electrical wire length connecting electrical components was minimal because all materials were housed in the aluminum “bear box.”

Photo Enumeration

We counted the number of fish passing upstream and summarized the counts on 1-minute intervals. Counts were adjusted for fish leaving the streams by recording downstream movements and subtracting these from the counts of upstream passage (i.e., # upstream - # downstream/min). We randomly selected 10 days from each stream (if available) to enumerate daily salmon abundance. We only used days that had complete or near complete 24-hr video records of fish movements.

RESULTS & DISCUSSION

Video Monitoring Setup

We believe that our photo-enumeration method can adequately capture the timing and abundance of salmon within tributaries. Although we did not formally compare different methods, such as weir or tower surveys, with our method, the clarity of the digital images and the ability to review video many times likely provided an accurate estimation of abundance. Nevertheless, there are advantages and disadvantages to different parts of the camera setup, and we will discuss those below.

Although the photo-enumeration method was able to reduce total sampling effort, it still required a considerable amount of effort to enumerate salmon. Sampling effort (time) was decreased by approximately $\frac{1}{2}$ to $\frac{1}{3}$ depending on salmon abundance and movements (e.g., 24 hours of video required approximately 8-12 actual hours to enumerate).

The addition of the lighting system provided sufficient illumination during low light periods to count salmon moving past the substrate panel. The benefits of the lighting system did come with some drawbacks, which need to be considered. First, even though the power requirements were minimal for the LED lights, any additional power usage needs to be evaluated and additional solar panels may be necessary to charge the battery bank. This becomes more of an issue as daylight decreases during the later spawning season. Second, the need for maintenance increased with the addition of the lights. It was important to clear debris and reattach lights if they became loosened. The lights were submersible, but it was important to encapsulate the lights within the vinyl tubing. The tubing protected the lights from bears and reduced the strain on the electrical wiring.

The camera and DVR adequately recorded streams that had approximate widths ≤ 10 m. At streams with widths ≥ 10 m (i.e., O'Malley Creek), the video was difficult to focus and was more pixilated compared to streams with smaller fields of view. Future efforts might want to consider higher quality camera and recording equipment in order to successfully capture salmon movements at larger streams. But, it will be important to consider how this will affect power consumption and memory requirements.

Once in place, the entire autonomous counting system required little maintenance. Surprisingly, we did not have any incidences in which a bear disturbed the camera system or the substrate panels. On rare occasions, bears either purposely or unknowingly dislodge the lights from the substrate panels. This required relatively little effort to fix. In all, the maintenance of the entire system was low. Nevertheless, we recommend the following for future projects involving the autonomous counting station. First, visit each camera system either daily or every two days, which will reduce potential data loss. Second, provide adequate power supply and recharging capacity. Most of our data loss occurred because our camera system and lighting system failed due to loss of power.

Daily Escapement

We retroactively counted the number of salmon that traveled upstream and downstream past the substrate panels. We determined the daily escapement total by subtracting the daily downstream total from the daily upstream total. Using this method, we estimated daily escapement for 12 days on CC and 10 days on MC (Table 1).

Daily upstream and downstream movement totals were highly correlated within the same day ($r = 0.86$). We often observed large downstream movements of fish within hours of large upstream movements, and in many cases, bears were seen on video chasing

the salmon downstream. Because salmon often left the stream, the daily escapement totals were much lower than the total number of salmon that traveled upstream. For example, on 18 July at CC, 1915 salmon entered and 1780 exited the stream. The estimated daily escapement totals of 135 salmon on that day under-represents the actual number of salmon that used the system. Therefore, it is important to understand that daily escapement does not equal the total number of salmon that used the stream that day, but rather the net cumulative total of salmon that remained in the stream that day. Future work evaluating spawning sockeye salmon abundance within tributaries might want to consider understanding individual salmon movement rates in and out of the system. This could improve estimates of daily abundance, which could provide a better estimate of the number of salmon within the system than daily escapement.

Nocturnal & Diurnal Movements

We determined the rate of movements by salmon during diurnal and nocturnal periods (Fig. 3.2 and 3.3). At MC, salmon traveled at a rate of 1.3 fish/hr during the daytime and -11.0 fish/hr during nocturnal periods. At CC, salmon traveled at a rate of 9.9 fish/hr during the daytime and -4.7 fish/hr during the nocturnal periods. Negative numbers represent movement of fish out of the tributaries. Future work evaluating spawning sockeye salmon abundance within tributaries should consider monitoring both diurnal and nocturnal periods. Relying on the assumption of similar movement rates between the two periods could lead to erroneous conclusions. In both MC and CC, we would have overestimated daily escapement without this knowledge.

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Table 3.1. Daily salmon movements estimated using the autonomous counting station at Canyon and Meadow Creeks, Karluk Lake, Alaska. Escapement total equals the number of salmon that traveled upstream minus the number of salmon that traveled downstream past the substrate panels.

Stream	Date	Daily Movements		
		Up-stream	Down-stream	Escapement Total
Canyon	July 16	1275	1468	-193
	July 17	229	301	-72
	July 18	1915	1780	135
	July 19	1457	1250	207
	July 24	768	313	455
	July 26	614	751	-137
	July 27	2090	1603	487
	July 28	910	725	185
	July 29	1713	828	885
	August 3	383	540	-157
	August 9	371	407	-36
	August 20	163	152	11
	Meadow	July 15	596	960
July 16		5175	3228	1947
July 17		573	1677	-1104
July 18		77	222	-145
July 19		604	468	136
July 20		1750	1623	127
July 21		719	639	80
July 25		838	1042	-204
July 26		612	654	-42
July 27		498	1309	-811

Figure 3.1. Autonomous video counting tower deployed at Meadow Creek, Karluk Lake, Alaska, to record salmon movements.



Figure 3.2. Estimated diurnal and nocturnal escapement totals per day of spawning salmon at Canyon Creek, Karluk Lake, Alaska, USA. Negative values indicate salmon leaving the stream.

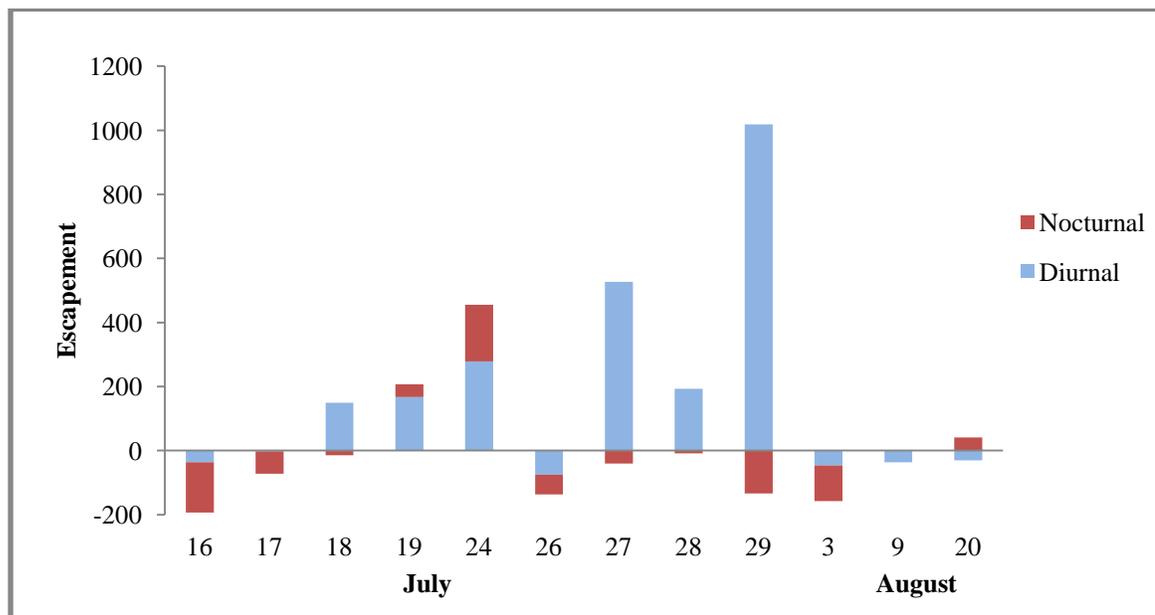
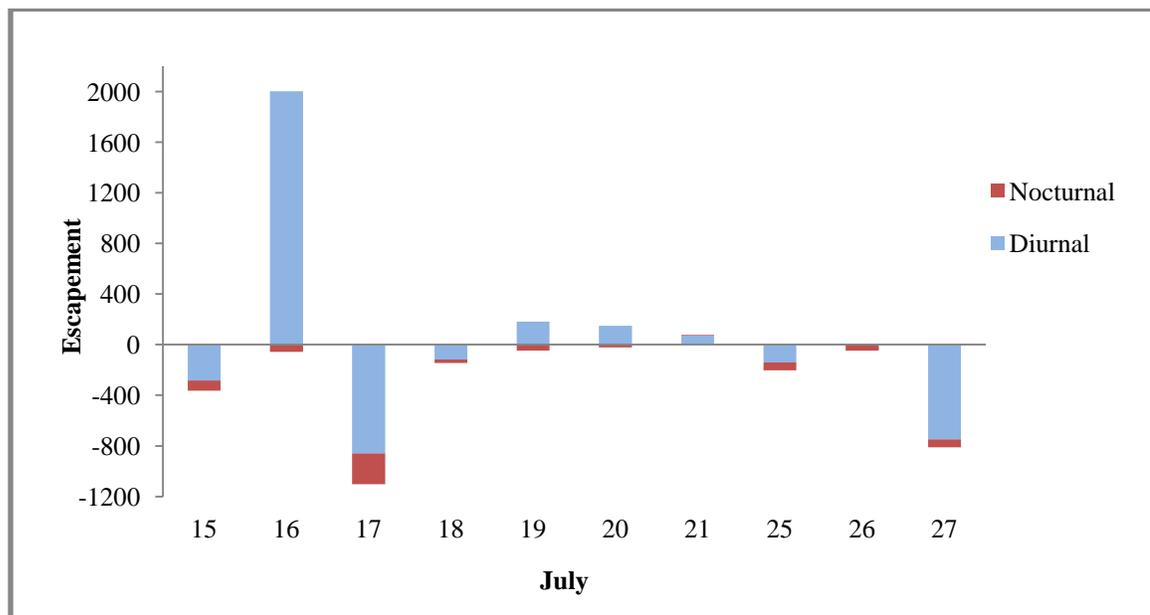


Figure 3.3. Estimated diurnal and nocturnal escapement totals per day of spawning salmon at Meadow Creek, Karluk Lake, Alaska, USA. Negative values indicate salmon leaving the stream.



THESIS CONCLUSION

Patterns of space use by animals are complex and driven by varying life-history objectives, however, many studies investigating space use by animals using remotely-sensed locations do not differentiate among locations that are used to satisfy different life-history requirements or locations that are used incidentally (Beyer *et al.* 2010). Interpretation of occupancy as a homogenous form of use limits our understanding of the mechanisms that influence space use and likely provides less insightful results about habitat features that promote fitness of individuals and persistence of populations (Beyer *et al.* 2010; Kertson & Marzluff 2010). This thesis examined the link between behavior and animal locations gathered via GPS technology, and we documented that bedding behavior used by brown bears could be accurately identified. Furthermore, we documented scale-dependent patterns of habitat selection at bedding sites, and these results suggested that bottom-up resources (i.e., food) were the most limiting resource for brown bears in our study area relative to top-down limitations (i.e., shelter and mortality risk).

We also demonstrated an approach that used remotely-sensed bear locations to collect fecal samples in order to estimate food habitat of brown bears, and we used this information to help refine dynamic patterns of resource availability. We documented that, indeed, the timing and use of food items directed patterns of space use and habitat selection by female brown bears. In addition, we showed that foraging strategies differed among individuals and that this variation likely was related to maternal status and differing strategies for optimizing mass gains.

On Kodiak, a wide variety of food items directed the space use and habitat selection patterns of bears, and thus understanding the timing and distribution of these food items is crucial for their conservation efforts. Our wildlife habitat analysis of space use directly linked patterns of habitat selection to food items use, which provided stronger inferential power for identifying the motivation directing these patterns. Bears were highly variable in resources selection suggesting that food item use was highly individualistic, and this life history trait is likely important for the health and productivity for brown bears. Therefore, we suggest that more attention be given to spatial-temporal patterns in food resources affecting bottom-up regulation in the population. Specifically, future efforts should consider incorporating measures of both productivity and abundance of important foods (i.e., berries/roots and salmon) into wildlife habitat models. Such an approach is necessary for understanding and accurately predicting the effects of changing environment on populations.

Overall, this work provides a better understanding of the mechanisms that shape resource selection and spatial ecology of female brown bears in southwestern Kodiak Island, Alaska. This information will assist in managing Kodiak National Wildlife Refuge lands with increasing potential for development and human activities such as bear-viewing tourism. A more comprehensive understanding of resource and space needs, particularly of females, can help managers to guide development in ways that minimize potential impact on population productivity and increase safety for both humans and bears.

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APPENDIX

Appendix A. Summary of vegetation community within generalized land cover classes on Kodiak Island, Alaska. The data were collected at bear use (feeding and bedding) and random locations (n) using point-intercept method. Bold percentages delineate the 3 highest proportions of each notable forage item.

		<u>Cover Class</u>											
		Birch-Cottonwood Forest	Open Alder	Dense Alder	Willow	Salmon-Elderberry	Alpine Tundra	Lowland Heath	Alpine Forb	Forb-Graminoid Meadow	Shrub-Graminoid Wetland	Water	Bare Rock
		n = 120	50	51	76	141	109	17	55	55	16	1	2
<u>General</u>	<u>Plant Name</u>	<u>Understory (%)</u>											
Tree	<i>Betula kenaica</i>	1.2	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Populus balsamifera</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Shrub (Tall)	<i>Alnus crispa</i>	0.3	6.7	3.4	0.3	4.7	0.2	0.0	0.1	0.8	0.0	0.0	0.0
Willows	<i>Salix spp.</i>	3.4	2.1	0.2	17.7	0.1	1.3	3.9	2.4	0.9	7.0	0.0	0.0
Small/Dwarf Shrub*		0.2	2.1	0.0	0.5	0.1	7.3	2.0	6.6	0.5	11.0	0.0	0.0
Fern		48.8	40.9	48.7	27.6	62.8	2.1	0.1	8.2	23.5	0.5	0.0	0.0
Graminoid*		49.1	40.1	25.1	57.3	28.8	24.3	31.3	50.3	63.3	79.0	0.0	2.4
Tundra/Heath*		1.1	1.1	1.1	4.6	0.1	69.3	116.8	16.5	2.1	39.6	0.0	6.1
Forbs*		92.5	81.3	25.4	88.7	25.2	57.6	37.2	112.3	118.1	27.9	0.0	24.4
Notable Bear Foods ^a													
	Graminoid <i>Carex spp.</i>	2.4	3.7	1.8	6.6	0.2	18.7	13.9	34.9	5.9	43.9	0.0	2.4
	Herbacous <i>Angelica spp.</i>	12.6	6.3	2.9	9.9	1.6	1.9	0.9	5.0	9.9	2.3	0.0	0.0
	<i>Equisetum spp.</i>	8.4	0.8	0.5	12.9	0.2	0.1	5.6	0.3	5.8	17.2	0.0	0.0
	<i>Heraculum lanatum</i>	9.4	11.8	5.1	5.3	3.6	0.0	0.0	1.5	7.4	0.2	0.0	0.0
	<i>Lupinus nootkatensis</i>	0.2	0.4	0.0	0.4	0.0	5.8	2.6	4.1	0.5	1.1	0.0	3.7
	<i>Urtica lyallii</i>	11.8	4.7	4.3	7.0	4.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0
	Fruit <i>Ericaceae spp. (Berry-Producing)*</i>	0.8	0.8	0.6	3.7	0.0	37.1	84.9	7.9	2.0	31.1	0.0	3.7
	<i>Rubus spectabilis</i>	1.0	13.5	12.0	1.0	23.8	0.2	0.0	0.7	3.8	0.0	0.0	0.0
	<i>Sambucus racemosa</i>	1.6	5.1	11.7	0.5	15.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
Non-Vegetation	Bed Rock / Talus	0.5	0.8	0.3	1.3	0.4	12.4	0.0	6.8	1.2	0.0	0.0	76.8
	Woody Stems	4.0	5.2	10.4	5.7	6.7	0.0	0.3	0.2	0.3	0.0	0.0	0.0
		<u>Overstory (%)</u>											
Tree	<i>Betula kenaica</i>	22.0	0.0	0.3	2.7	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0
	<i>Populus balsamifera</i>	18.4	1.5	1.1	0.6	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Shrub (Tall)	<i>Alnus crispa</i>	4.0	25.3	72.3	0.8	37.4	0.1	0.0	0.1	3.5	0.0	0.0	0.0
Willows	<i>Salix spp.</i>	13.4	1.8	0.4	34.2	0.5	0.0	0.0	0.9	1.4	0.0	0.0	0.0
Fern		0.9	0.1	0.2	0.3	1.7	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Graminoid*		0.8	0.1	0.4	0.3	1.1	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Forbs*		0.0	0.4	0.5	0.2	0.4	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Notable Bear Forage													
	Fruit <i>Rubus spectabilis</i>	0.1	0.0	0.2	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Sambucus racemosa</i>	1.1	3.1	12.1	0.4	18.6	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Canopy Cover	Total Overstory (%) ^{a,b}	57.1	31.7	80.9	38.6	56.3	0.2	0.0	1.2	6.5	0.0	0.0	0.0

* - Multiple species aggregated into a generalized class, therefore associated number should be interpreted as a scale rather than a percentage.

^a - Species percentages included in general classes above (except *Equisetum spp.*)

^b - Includes vegetative and non-vegetative items above 1.5m height.

Appendix B. Individual parameter estimates from 30 female brown bears used to describe foraging habitat selection on Kodiak Island, Alaska.

Bear ID	SRI X P_{spring}	elev X P_{spring}	elev X P_{summer}	dist.stream $X P_{early}$	dist.stream $X P_{late}$	root.berry $X P_{early}$	root.berry $X P_{early}$
517*	19.3	-3.5	0.5	-13.2	-45.6	-2.5	-0.1
520	1.0	2.2	-0.7	-17.4	-24.0	-1.2	-0.7
527**	-4.4	4.0	-0.6	-28.1	-61.9	-1.7	1.7
529	-6.8	-1.5	-4.0	-7.6	-27.9	-0.3	0.1
530	2.6	-2.7	-7.9	-9.6	-46.8	-1.6	0.2
531	20.5	-9.5	-8.0	-44.6	-49.6	-1.7	0.1
532**	0.1	18.9	1.9	-0.5	3.8	2.0	NA
533	7.2	-3.8	-0.1	-26.4	-44.0	-1.1	-0.1
534	3.1	-3.5	-2.3	1.4	-8.5	-0.6	1.4
535	-8.0	-4.3	-1.0	-18.7	-37.8	-2.1	1.0
536	-3.9	-0.6	-6.2	-53.0	-15.3	-1.5	1.1
537	4.5	0.3	-1.9	-2.3	-27.2	-0.4	-1.6
538	-2.9	-0.8	6.2	-44.1	-14.6	-1.5	0.0
540	-0.7	-3.2	-6.7	-78.9	-172.6	0.1	NA
543	17.1	-11.2	-17.5	-17.7	2.1	-2.1	NA
545	2.1	0.5	5.1	-0.2	-17.8	-1.1	0.0
546	1.8	5.3	6.9	-20.3	-87.7	-0.2	0.7
547	-0.9	5.3	-2.5	-32.7	-24.0	-0.7	1.2
548	6.0	-2.4	1.0	-13.4	-23.4	-1.1	-0.5
550*	-2.4	-4.7	1.0	-6.3	-37.1	-1.3	-1.4
553	0.5	0.0	-10.4	-0.4	-5.4	-1.3	1.1
554	-3.9	-5.7	-2.9	-4.2	-28.6	-1.4	NA
555	-0.2	-16.6	1.3	3.0	NA	NA	NA
556	7.1	0.0	2.2	-14.3	-50.1	-0.3	NA
558	-4.2	-6.9	-1.8	-28.6	-26.4	0.0	-0.1
559	0.9	-8.3	-9.5	-65.5	-29.1	-1.9	-0.7
560	-10.1	-6.8	-3.8	-2.3	-7.2	-0.4	1.0
561	14.0	-7.5	-1.0	-12.6	-8.2	0.5	0.3
564	7.1	-10.3	-11.5	-18.1	-13.3	0.3	NA
565	-1.1	-3.6	-7.9	-0.8	-4.7	-0.1	-0.9

* - Represents female with cubs > 1 year old

** - Represents female with cubs of the year

NA - No data available to estimate parameter during that period

Appendix C. Individual parameter estimates from 30 female brown bears used to describe bedding habitat selection at the home range scale on Kodiak Island, Alaska.

Bear ID	SRI X	elev X	elev X	dist.stream X	dist.stream X	root.berry X	root.berry X	hillshade X	forest X	tall.shrub	tall.shrub	slope
	P_{spring}	P_{spring}	P_{summer}	P_{early}	P_{late}	P_{early}	P_{early}	P_{day}	P_{day}	X P_{day}	X P_{night}	
517*	25.6	-10.0	1.6	-13.0	-36.5	-5.5	-0.7	-1.7	0.6	-0.3	-0.7	0.6
520	-3.6	2.5	-1.8	-9.7	-6.9	-1.2	0.1	-1.6	1.2	0.7	-0.3	-0.1
527**	-5.0	2.8	-3.2	-39.3	-31.5	-1.8	2.5	3.1	0.2	0.0	-0.1	-1.0
529	-11.0	-4.4	-3.8	-0.2	-25.0	-1.5	1.6	0.8	1.2	1.1	1.1	-2.1
530	3.2	-4.2	-9.2	-11.4	-49.7	-2.0	-0.5	-1.1	1.3	0.2	-0.4	-5.6
531	35.5	-11.6	-46.0	-25.3	-37.7	-1.5	1.1	1.0	-0.3	-0.4	-0.5	-3.3
532**	-1.0	-3.8	1.5	-7.0	-9.2	-0.1	-0.4	4.6	0.9	-0.1	-0.3	0.9
533	10.4	-6.4	0.7	-32.3	-37.4	-0.8	0.5	2.3	1.4	1.3	0.7	-6.1
534	5.5	-3.9	-1.5	2.2	-9.8	-0.8	1.8	1.4	1.5	0.7	0.1	-1.4
535	-7.5	-5.6	-0.9	-16.8	-32.5	-1.8	0.8	1.3	1.4	0.8	0.5	-2.4
536	-3.7	0.5	-7.0	-36.0	-12.0	-1.4	-0.2	0.9	0.0	0.5	1.0	-4.8
537	4.9	0.5	-1.3	-4.6	-16.0	-0.6	-0.7	-0.7	0.7	-0.4	-0.9	-0.7
538	-8.2	-0.8	6.9	-41.1	-10.7	-1.7	-0.5	1.3	0.5	0.2	0.0	-1.0
540	7.8	-3.5	-49.0	-81.8	-117.4	-1.1	NA	3.1	-1.3	-1.1	0.7	-2.7
543	18.5	-12.7	-18.0	-16.8	1.4	-2.7	NA	-2.6	0.9	0.4	0.7	-3.5
545	1.2	-0.9	8.3	3.7	-13.7	-1.4	0.1	1.7	0.8	-0.2	-0.5	0.8
546	3.2	3.3	5.5	-15.3	-70.4	-0.4	NA	-2.4	-0.1	-0.6	-0.5	0.2
547	-0.3	6.0	-1.1	-50.7	-17.2	0.3	1.1	-0.4	0.9	0.3	-0.2	-1.5
548	7.8	-3.7	0.2	-13.0	-20.7	-1.0	0.2	-2.3	1.4	1.0	0.5	-0.3
550*	-0.5	-1.2	3.6	0.7	-20.0	-1.0	-0.7	-4.4	0.6	0.1	-1.0	-2.0
553	0.0	1.1	-7.0	-1.3	-5.3	-0.6	0.9	-0.3	2.2	0.2	-0.4	-3.7
554	0.3	-3.3	-2.5	-2.5	-34.0	NA	NA	0.7	2.2	0.7	-0.1	0.3
555	-0.9	-8.6	-1.4	4.9	NA	NA	NA	2.2	1.5	0.3	-0.7	-1.0
556	5.3	1.7	3.4	-13.5	-108.0	-0.6	NA	-2.2	0.2	-0.7	-1.3	-1.6
558	-6.7	-11.2	-7.6	-40.3	-27.6	-0.3	-1.2	1.8	1.3	0.6	0.5	-4.1
559	2.1	-6.4	-9.6	-35.5	-27.4	-1.9	-0.7	1.1	1.2	0.0	-0.2	-10.8
560	-9.7	-5.9	-4.9	-0.6	-5.6	-0.1	0.1	-0.5	0.5	0.5	0.2	-2.1
561	14.0	-7.1	-3.2	-12.4	-7.6	0.5	0.1	2.8	0.9	1.1	1.3	0.5
564	5.8	-10.7	-8.3	-7.9	NA	NA	NA	0.1	1.3	0.7	-0.3	-5.3
565	-1.1	-5.3	-9.2	0.4	-5.9	0.0	-0.5	-1.2	1.6	0.8	0.5	-4.4

* - Represents female with cubs > 1 year old

** - Represents female with cubs of the year

NA - No data available to estimate parameter during that period

Appendix D. Individual parameter estimates from 10 female brown bears used to describe micro-site bed site habitat selection on Kodiak Island, Alaska.

Bear ID	dist. stream	forb. cov	sedge. cov	berry. cov	canopy.cov x day	stem	elderberry. cov	micro. topo
517*	-23.0	-2.0	-3.5	0.8	0.9	4.1	5.4	2.6
520	1.7	0.9	-6.1	2.6	2.9	3.9	1.8	20.7
530	179.6	-0.3	-592.6	NA	5.6	6.5	1.3	NA
532**	-142.6	-5.2	1.3	0.1	2.3	4.3	-0.8	21.2
554	88.8	3.7	2.4	NA	2.0	2.9	0.1	19.2
555	25.7	-0.7	3.0	NA	39.0	1.9	1.4	20.0
558	-95.6	-3.1	-4.3	-2.5	10.2	10.2	3.3	NA
560	-21.7	NA	NA	-0.1	4.0	5.8	-2.6	20.2
561	-49.3	0.6	-0.9	0.2	22.9	3.6	2.9	18.2
564	-118.6	0.8	-6.9	NA	2.0	1.1	5.5	NA

* - Represents female with cubs > 1 year old

** - Represents female with cubs of the year

NA - No data available to estimate parameter during that period