

**RESOURCE SELECTION AND MOVEMENT PATTERNS  
BY KODIAK ISLAND BROWN BEARS**

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

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by

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## ABSTRACT

Animal movement and resource selection across the landscape plays a critical role in ecological processes, wildlife management, and conservation efforts. Understanding how animals move through landscapes to exploit heterogeneously distributed resources is critical to their conservation and management. This is becoming increasingly important in light of mounting development activities, climate change, and environmental changes that could disrupt access to resources and landscape connectivity.

The ability of an animal to traverse the landscape to access resources and their decisions affecting movement patterns have implications for individual fitness and the conservation of populations. Understanding these decisions and the factors driving consequent space-use patterns have important conservation implications. Resource selection studies have emerged as a valuable tool for understanding these phenomena. Nevertheless, investigations into animal movement and resource selection are presented with some challenges. Among these challenges are identifying predictive environmental covariates, scale, defining availability, modeling and statistical constraints, temporal fluxes in resources, and the varying needs and objectives of animals across seasons.

This dissertation consists of four chapters investigating Kodiak brown bear (*Ursus arctos middendorffi*) movements and resource selection. We explore brown bear exploitation of spatio-temporal patterns of sockeye salmon (*Oncorhynchus nerka*) spawning across the landscape (Chapter 1); characterization of brown bear travel paths to move among and exploit sockeye salmon spawning areas across the landscape; (Chapter 2); the influence of local sockeye salmon spawning timing and abundance on Kodiak brown bear patterns of exploitation (Chapter 3); and post-den emergence habitat selection (Chapter 4).

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Finally, we would like to express our deepest gratitude to the bears of Kodiak and Kamchatka. They put up with us, Tip and Bill, for over two decades and offered us a peek into their wondrous lives. Our hope is that those responsible for their conservation and the stewardship of the wild lands, waters, and ecosystems that support them will stay focused on this mission.

## DEDICATION

This work is dedicated to the cherished memory of Tip (Moon) Leacock, the essence of *မေတ္တာ* (*metta – loving kindness*).



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## STATEMENT OF CONTRIBUTION

Chapter 1 and Chapter 3: William B. Leacock, William W. Deacy, and Jonathon Armstrong conceived of the research. William Leacock and William Deacy designed the methodology and collected the data. William Leacock secured funding and support for all fieldwork, field staff, and supervised the project. William Deacy, William Leacock, and Jonathon Armstrong carried out analyses. All authors were responsible for writing.

## CHAPTER 1

### **KODIAK BROWN BEARS SURF THE SALMON RED WAVE: DIRECT EVIDENCE FROM GPS COLLARED INDIVIDUALS**

William Deacy, William Leacock, Jonathan B. Armstrong, and Jack A. Stanford.  
*Ecology*, 97(5), 2016, pp. 1091–1098.

#### **ABSTRACT**

A key constraint faced by consumers is achieving a positive energy balance in the face of temporal variation in foraging opportunities. Recent work has shown that spatial heterogeneity in resource phenology can buffer mobile consumers from this constraint by allowing them to track changes in resource availability across space. For example, salmon populations spawn asynchronously across watersheds, causing high quality foraging opportunities to propagate across the landscape, prolonging the availability of salmon at the regional scale. However, we know little about how individual consumers integrate across phenological variation or the benefits they receive by doing so. Here, we present direct evidence that individual brown bears track spatial variation in salmon phenology. Data from 40 GPS collared brown bears show that bears visited multiple spawning sites in synchrony with the order of spawning phenology. The number of sites used was correlated with the number of days a bear exploited salmon, suggesting the phenological variation in the study area influenced bear access to salmon, a resource which strongly influences bear fitness. Fisheries managers attempting to maximize harvest while maintaining ecosystem function



should strive to protect the population diversity that underlies the phenological variation used by wildlife consumers.

## INTRODUCTION

One of the central themes in ecological theory is that biodiversity enhances and stabilizes ecosystem services (Tilman et al. 1996, Kennedy et al. 2002, Hooper et al. 2005). While most biodiversity research and conservation efforts have focused on species diversity, finer levels of biodiversity (i.e., intraspecific diversity) are far more threatened; for example, extinction rates for populations are roughly 1000- times higher than those for species (Hughes et al. 1997). Thus, a critical challenge in ecology is to understand the functional significance of intraspecific diversity.

There has been recent interest in the potential for intraspecific variation to generate “portfolio effects,” in which asynchronous dynamics among populations have emergent properties expressed at higher levels of biological organization (Schindler et al. 2015). For example, asynchrony in the population dynamics of sockeye salmon (*Oncorhynchus nerka*) dampens levels of temporal variation expressed across the aggregate of populations. This can be seen in sockeye salmon stock complexes where the boom of one population compensates for the bust in another, resulting in more stable commercial fisheries harvests (Schindler et al. 2010). Asynchrony among populations occurs not only in the interannual trends of abundance, but also in the intraannual timing of life- cycle events (i.e., phenology). For example, populations that occur in different habitats may exhibit different seasonal patterns of birth, migration, and reproduction, often due to local adaptation. There is increasing interest in whether phenological asynchrony among populations (or other scales of biological organization) can generate ecologically significant emergent properties. For example, an

accumulating body of evidence shows that asynchronous phenology among prey resources can have strong positive effects on wide-ranging consumers by triggering resource waves (Armstrong et al. 2016).

Resource waves are important when a prey species is only available (or is of high quality) during a specific developmental stage and its phenology varies across prey subpopulations (variation at other levels of biological organization may also cause resource waves). For example, migrating ungulates and waterfowl take advantage of spatial variation in the timing of spring vegetation growth (the so called “green wave”) in order to consume high- quality forage for a longer period than is available at a single foraging site (Sawyer and Kauffman 2011, van Wijk et al. 2012). Similarly, surf scoters (*Melanitta perspicillata*) and rainbow trout (*O. mykiss*) track spatial variation in spawning phenology of herring (*Clupea pallasii*) and sockeye salmon (*O. nerka*), respectively, to extend their access to energy- dense eggs (Ruff et al. 2011, Lok et al. 2012). Although there is rapidly increasing interest in this topic, we often lack data to address how individuals track resources. Commonly, tracking is inferred from consumer distributional data (Fryxell et al. 2004, Lok et al. 2012, Schindler et al. 2013) or assumed based on the existence of a resource wave (Coogan et al. 2012). Using these methods, it is difficult to determine whether changes in consumer distribution and abundance are due to individuals aggregating around a local resource (only using a single prey subpopulation) or individuals tracking resources across the landscape (using several prey populations). Individual movement data is needed to provide conclusive evidence of resource tracking and to directly quantify the functional significance of resource waves to consumers.

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Populations of spawning Pacific salmon (*Oncorhynchus* spp.) provide an example of how population diversity can prolong the temporal extent of prey availability across landscapes (Schindler et al. 2010, 2013, Ruff et al. 2011). Salmon breeding phenology is related to freshwater thermal regimes that vary spatially due to heterogeneity in

geomorphology and hydrology (Lisi et al. 2013). Across an aggregate of salmon populations, spawning activity often spans several months, however, each individual population may only spawn for as little as two to three weeks (Gende et al. 2004, Carlson et al. 2007, Schindler et al. 2010). These brief periods of salmon spawning are spread across space and through time, creating resource waves that potentially benefit mobile consumers, however, the actual benefit depends on the degree to which mobile consumers can track the shifting mosaic of salmon resources.

Of the large number of predators and scavengers that feed on seasonally available spawning salmon (Shardlow and Hyatt 2013), brown bears (*Ursus arctos*) are perhaps the most iconic and have a well- documented dependence on salmon; fecundity, body size, and population density are all strongly correlated with salmon consumption (Hilderbrand et al. 1999). Given the importance of salmon to bears, their keen sensory abilities, and their mobility, one would expect them to be highly capable of tracking spatiotemporal variation in salmon abundance across landscapes. Schindler et al. (2013) revealed strongly suggestive evidence that bears surf salmon resource waves and the potential for this behavior to prolong foraging opportunities for bears. However, no direct evidence exists nor do we understand the degree to which individual bears track salmon, or how much individual variation exists in tracking behavior. In this paper, we (1) quantify the salmon resource wave, (2) track individual bear movements in relation to the wave, and (3) quantify the degree to which individual bears extend their foraging opportunities by surfing the resource wave. We provide the first direct evidence of bears tracking salmon phenology and show that salmon phenological diversity prolongs the duration of bear foraging opportunities by an average of 1.7 times.

## METHODS

### *Study site*

This work was conducted in southwestern Kodiak Island, in the western Gulf of Alaska (Appendix A). The Kodiak Archipelago has an estimated population of 3500 brown bears, hundreds of rivers, lake shoals, and streams used by spawning Pacific salmon (*Oncorhynchus* spp.), and limited human activity. The area has a rich history of bear–salmon research (Gard 1971, Barnes 1990, Van Daele et al. 2013). Barnes (1990) showed the home ranges of bears in southwest (SW) Kodiak often overlap multiple drainages and many salmon spawning sites, providing the first evidence that individual bears may exploit multiple salmon populations. The majority of the SW portion of the island is within the Kodiak National Wildlife Refuge, which is managed by the U.S. Fish and Wildlife Service. Human activity in the study area is limited and consists primarily of sport fishers, bear viewers, and hunters. The bears on the Kodiak archipelago are hunted during the fall and spring each year. Approximately 190 bears were harvested annually from 2000–2009.

Although five species of salmon spawn in SW Kodiak waters, sockeye and pink salmon (*Oncorhynchus gorbuscha*) are the most abundant (Van Daele et al. 2013). From 2000–2009, over half of the salmon returns for the Kodiak Archipelago occurred in the SW region, with an average escapement (fish remaining after harvest) of over 3.2 million. Pink salmon spawn primarily in main stem rivers and estuaries at the mouths of rivers. Sockeye salmon spawn mainly in headwater streams, on lake beaches with interstitial flow of groundwater and in lake-outlet rivers. Most of the stream habitats are narrow (<5 m), shallow (<0.5 m), and flow into lakes, rivers, or directly into the ocean. Sockeye juveniles typically rear in lakes downstream of tributary spawning streams. Four large, salmon-producing,

stream–lake systems exist in the study area: Karluk, Red, Akalura, and Frazer. Preliminary results from ongoing genetic studies have detected population genetic differences in spawning sockeye salmon at the level of habitat types within a watershed (i.e., river, lake shore, tributary stream), but not within a habitat type (e.g., tributary streams within the Karluk watershed; Jeff Olson, personal communication).

In addition to salmon, bears routinely consume several species of berries, including red elderberry (*Sambucus racemosa* L.), salmonberry (*Rubus spectabilis* Pursh), crowberry (*Empetrum nigrum* L.), and blueberry (*Vaccinium* spp.) and many species of grasses, sedges, and forbs (Van Daele et al. 2013).

#### ***Variation in timing of salmon availability for bears***

We used the Alaska Anadromous Streams Catalog (AASC) and field observations to identify the water bodies in SW Kodiak where bears have access to salmon (Figure 1.1). We found seven rivers and 68 streams listed in the AASC as salmon spawning habitat. The AASC does not list beach spawning sites; we identified 19 beach sites where sockeye salmon spawn through weekly aerial surveys. In addition to spawning sites, we included one site where a salmon- passable cataract called Dog Salmon Falls makes migrating salmon vulnerable to bear predation. These 95 sites include all of the sites where bears can access salmon within the study area, however, bear telemetry data suggests only a subset of these sites are regularly visited by bears. We characterized the average spawning phenology at 32 of these sites using 9 years of aerial, boat, and ground observations (William Leacock, unpublished data). The order of salmon availability we observed among habitat types (the falls, lake–tributary streams, lake–outlet rivers, lake beaches) matched the patterns

documented in similar systems driven by water temperature variation (Doctor et al. 2010, Schindler et al. 2010).

### ***Bear movements in relation to salmon abundance***

A challenge in many behavioral studies is to infer foraging behavior from movement and habitat use when data on trophic resources are not available across the entire landscape. Although we could not determine the timing of salmon availability at every site across the landscape, we characterized salmon phenology data across a large number of spawning sites ( $n = 32$ ; 34% of all sites). Inferring bear foraging opportunity from movement behavior would be problematic if bears resided at salmon spawning sites for purposes other than salmon foraging. To test whether this was the case, we monitored streams with remote cameras and evaluated how bear presence responded to salmon abundance. In 2013, we deployed one to three time-lapse trail cameras (PC800, Reconyx, Holmen, WI, USA) along six streams in the study area. The cameras were programmed to take a photo every 5 min, 24 h/d from June through September. We counted the number of bears in each time-lapse frame, counting sows with cubs as a single independent bear. Similar to the results of Schindler et al. (2013) and Quinn et al. (2014), the peak spawning date at each site was positively correlated with the median date of bear detections ( $R^2 = 0.33$ , Appendix B). This indicated that SW Kodiak bears responded to seasonal changes in salmon availability. Most importantly, bears were virtually absent ( $0.6 \pm 1.8$  bear detections  $\cdot$  d<sup>-1</sup>  $\cdot$  stream<sup>-1</sup>; mean  $\pm$  SD) when salmon were not spawning, but became ephemerally super abundant ( $36.6 \pm 66.8$  detections  $\cdot$  d<sup>-1</sup>  $\cdot$  stream<sup>-1</sup>) during the salmon run. These data, in addition to prior studies (Schindler et al. 2013, Shardlow and Hyatt 2013) confirm that it is reasonable to assume that (1) bears present at spawning salmon sites were foraging on salmon and (2) the number of

days spent at salmon sites accurately reflected the duration of salmon foraging opportunities for bears. To account for the occasional use of salmon spawning habitats as movement corridors, we differentiated between bear passage and residence by considering individuals to be exploiting salmon only when they exhibited GPS locations within 50 m of a salmon spawning site at least twice a day for at least 5 d in a year. For each bear, we calculated the number of salmon spawning sites attended and the total number of days spent foraging on salmon.

### *Movements of collared bears*

Seasonal changes in bear distribution (Appendix B) may be due to local bears aggregating at a nearby spawning site (only using a single salmon subpopulation) or individuals tracking salmon spawning phenology across the landscape (using multiple salmon populations). Distributional data cannot distinguish between these scenarios nor quantify the functional significance of salmon resource waves to bears; therefore, we collected movement data from individual bears using GPS collars.

We captured adult female brown bears in the SW region of Kodiak Island, Alaska by firing immobilization darts from a helicopter. We fitted each bear with a GPS radio collar programmed to record a location every hour from early June through mid- November. Collars contained a UHF (ultrahigh frequency) transmitter and were downloaded using an airplane fitted with a UHF receiver. From 2008 to 2014, 143 284 GPS locations were recorded from 43 individuals over 67 bear-years (some bears carried collars for more than 1 year). We screened GPS locations for accuracy, removing relocations with a positional dilution of precision (PDOP) greater than 10 (Lewis et al. 2007). We excluded bears from the analysis if their collars failed before acquiring at least 1500 relocations in a year. Following



these quality- control measures, 133 085 relocations from 52 bear-years and 40 unique bears remained for analysis.

To determine the order of habitat use for each bear, we first produced empirical cumulative distribution functions (ECDF) for each habitat and each bear. Next, we used the median date of each ECDF to determine the first and last habitat used by each of the bear-years where a bear used more than one habitat ( $N = 41$  bear-years). Finally, we tabulated these values in a contingency table and used a chi- squared test of independence ( $\alpha = 0.05$ ) to determine whether the pattern of habitat visit order was random ( $H_0$ ) or not ( $H_a$ ).

## RESULTS

Salmon were available to bears (i.e., on spawning grounds or migrating past the waterfall) at different times in different habitats. Median occupancy date for the waterfall, tributary streams, lake- outlet rivers, and lake beaches was 14 July, 3 August, 23 September, and 23 October, respectively (Figure 1.2). Most of the sites visited by bears were salmon spawning grounds, however, salmon availability to bears was further prolonged by point-habitat features that made fish vulnerable to predation. At the Lower Falls of the Dog Salmon River, a small waterfall where bears intercept salmon as they migrate upriver, salmon were available as early as 3 June. Thus, habitat heterogeneity and phenological diversity of salmon prolonged their duration of availability to bears from approximately 40 d for a single stock, to roughly 150 d for the aggregate.

We documented considerable variation in the number of spawning populations exploited by collared female bears. On average, each female bear exploited 3.1 populations of spawning salmon in a year (median = 3.0,  $n = 52$ ,  $SD = 1.5$ , Figure 1.4A). The maximum

used by a single bear was seven sites, while one bear used no salmon sites. In general, the order in which bears visited spawning sites matched the sequence of salmon run timing (Figure 1.3A,B); bears tended to visit habitats with early salmon availability first (falls and streams) and habitats with late availability last (river and lake beaches,  $\chi^2 = 31.7$ ,  $n = 41$ ,  $P < 0.0001$ , Appendix C). Furthermore, the median date that individual bears used the habitat with the latest availability (lake beaches) was 48 d later than the median date they used the site with earliest salmon availability (the Lower Dog Salmon Falls).

The mean number of days each bear exploited salmon was 67 ( $n = 52$ ,  $SD = 33.5$ ), whereas the average spawning population was only available for approximately 40 d. Seventy- three percent of bears spent more than 40 d fishing for salmon. Regression analysis indicates the number of spawning populations exploited was positively correlated with the number of days each bear fished (Figure 1.4B,  $R^2 = 0.36$ ,  $P < 0.0001$ ).

## DISCUSSION

Although each individual subpopulation spawned for a brief period (~40 d), spawning activity spanned several months across all of the salmon subpopulations. The timing of salmon availability varied by habitat: salmon first appeared while migrating past waterfalls, then while spawning in streams, rivers and, finally, lake beaches. Counts of bears from time-lapse images showed that bears were unlikely to be detected at streams when salmon were not spawning (0.6 detections/d) compared to when they were spawning (31 detections/d). Given this pattern, we used GPS relocations from collared female bears to indicate bear foraging behavior. These data showed the number of sites used by bears varied from zero to seven (mean = 3.1,  $SD = 1.5$ ) and they tended to visit sites in their order of availability, using the falls (available in June/July) an average of 48 d earlier than lake beaches (available

September/October). Although spawning salmon were only available at individual sites for ~40 d, bears foraged for an average of 67 d, 1.7× longer than if there was no variation in run timing. Ruff et al. (2011) documented a similar effect; rainbow trout in their study had access to salmon 1.5× longer due to phenological variation among salmon populations. The degree to which our collared bears moved among sites correlated with their access to salmon: as bears increased the number of sites they attended, they significantly prolonged their access to salmon ( $R^2 = 0.36$ ,  $P < 0.0001$ ). Given that a bear's consumption of abundant prey such as salmon is limited by duration of access (because of digestive constraints on foraging rates) rather than merely abundance, our results strongly suggest that bears directly benefit from salmon life history diversity. Because we only studied the foraging habits of female bears, the results of this study are likely conservative; females have smaller home ranges than males, particularly when they have cubs (Berns et al. 1980), and their smaller body sizes make them less dependent on high calorie foods such as salmon (Welch et al. 1997, Rode et al. 2001).

Population diversity in salmon and the corresponding asynchrony in spawn timing increases the duration of salmon availability for bears. In addition, physical features along salmon migration routes, such as waterfalls or cataracts, can extend the life history phases in which salmon are vulnerable to include not only spawning, but also migration to upstream spawning sites. While point features (e.g., McNeil and Brooks Falls, Alaska) are recognized as important because they make salmon vulnerable to bears in large rivers where they are otherwise inaccessible (Quinn et al. 2001, Peirce et al. 2013), their significance in regards to timing are much less appreciated. In the Karluk system, salmon were available at the Lower Falls of the Dog Salmon River almost a month before spawners in streams.

Loss of life history diversity has the potential to erode the ecosystem services important to humans. Schindler et al. (2010) simulated the effects of loss of population diversity on the reliability of commercial fishing harvests and found that population homogenization would result in ten times more frequent fisheries closures. Our results indicate that loss of population diversity would also affect wildlife consumers such as bears: the average bear in our study would have 48% less time to consume salmon if all of the salmon in our study area spawned at the same time. A challenge for fisheries management is to conserve diversity at the population level while managing harvest at coarser levels (i.e., watersheds consisting of dozens of populations). Population diversity is not explicitly considered in the maximum sustained yield paradigm of salmon fisheries management, yet it clearly mediates the long-term reliability of fisheries (Hilborn et al. 2003, Schindler et al. 2010) and likely the energy flows from fish to consumer species in freshwater food webs (Ruff et al. 2011, Schindler et al. 2013). Many salmon fisheries are temporally biased, substantially increasing harvest rates once escapement goals are met (Quinn et al. 2007). Given evidence for population-level variation in salmon migration phenology (Boatright et al. 2004, Doctor et al. 2010, McGlaufflin et al. 2011), temporally biased fisheries may diminish population diversity by selecting against stocks with late migration phenologies (Quinn et al. 2007), which are likely associated with late spawning phenologies and thus availability to bears (Boatright et al. 2004, Doctor et al. 2010).

Given the well-documented benefits of salmon consumption, it is interesting that several bears (23% of bear-years) used salmon for <40 d and one bear was never relocated within 50 m of a salmon site. An earlier study on the Kodiak Archipelago (Van Daele et al. 2013) found that salmon accounted for an average of 48% of assimilated diets of adult

female bears and 16% of females had diets consisting of less than 10% salmon (based on stable isotopes and mercury analysis). Some bears may eat few salmon because salmon availability varies across the study area. In some areas, a bear could attend multiple spawning sites with only short movements, while in others the costs of moving among sites are greater. It may also be a result of intraspecific competition at salmon sites; due to higher bear densities, there is a heightened risk of aggressive encounters (Gende and Quinn 2004) and infanticide for sows with cubs (Ben-David et al. 2004). This may cause some bears to eschew salmon for less energy-dense, but less risky, foods such as vegetation or berries.

Researchers have noted the amount of salmon consumed by bears varies by sex, age, and maternal status, with dominant males consuming the most salmon and subdominant bears the least (Van Daele et al. 2013). This may be due to allometric scaling between body mass and nutritional requirements (Welch et al. 1997, Rode et al. 2001), but likely also reflects the tendency for dominant bears to exclude less dominant bears from preferred salmon foraging sites (Gende and Quinn 2004). Although bears adopt strategies to limit competitive interactions at spawning sites, for example, by partitioning use across space and through time (Nevin and Gilbert 2005), competition may be reduced further when several populations of salmon are spawning at the same time in multiple locations. Thus, while phenological diversity increases the duration of salmon access for bears, this benefit may only be realized by the most dominant bears unless salmon are spawning across a sufficiently large area to limit competition. In this context, it is not surprising that 73% of tracked bears used at least one stream site, while only 10% used the Lower Falls, the site that provides the earliest access to salmon. The SW Kodiak Island study site has limited human development and recreational activity. In many other parts of Alaska, landscapes face increasing pressure

for resource and infrastructure development. Recent evidence suggests that such habitat alteration often results in permeable barriers that may maintain habitat connectivity, yet interfere with the ability of consumers to track resource waves (Sawyer et al. 2013). Bears in the most productive populations often rely on salmon for the majority of their annual energy intake (Hilderbrand et al. 1999). Our results suggest that tracking of phenologically diverse salmon populations plays an important role in allowing bears to acquire energy from ephemeral salmon resources. Human actions that reduce salmon population diversity or inhibit bear movements reduce the potential for bears to eat salmon, which would likely decrease bear population productivity (Hilderbrand et al. 1999). The corollary for salmon restoration efforts is that restoring salmon abundance with homogenous hatchery stocks, in heavily fragmented landscapes, is unlikely to restore the functional link between salmon and culturally, commercially, and ecologically important consumers such as brown bears.

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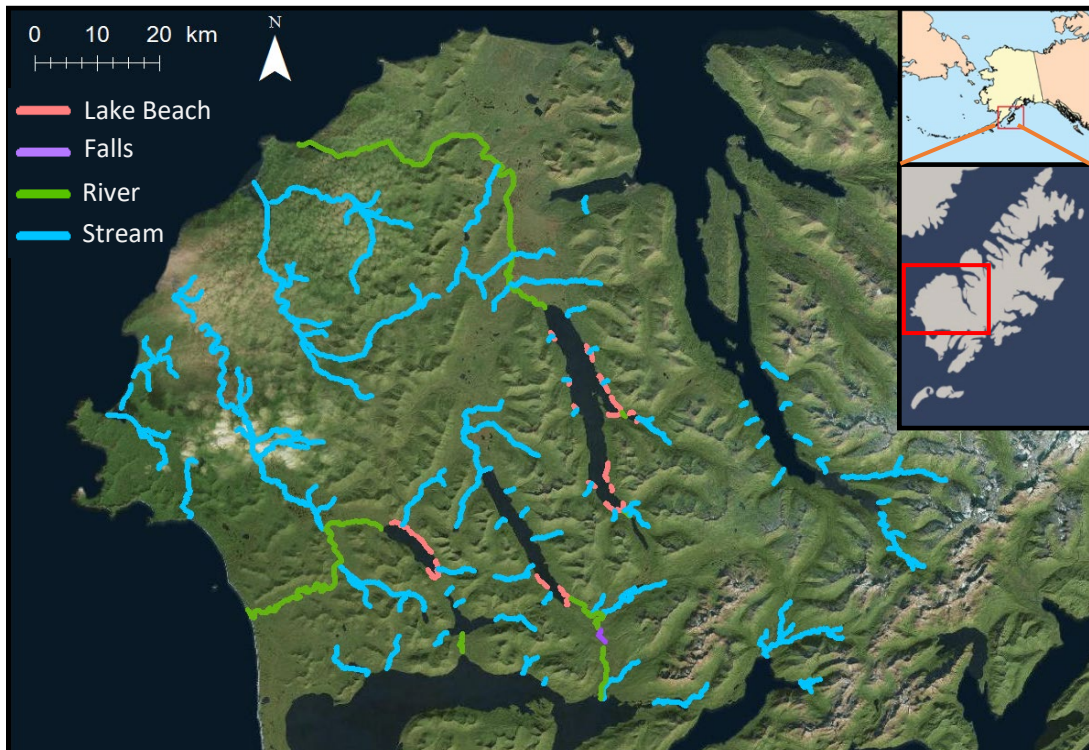


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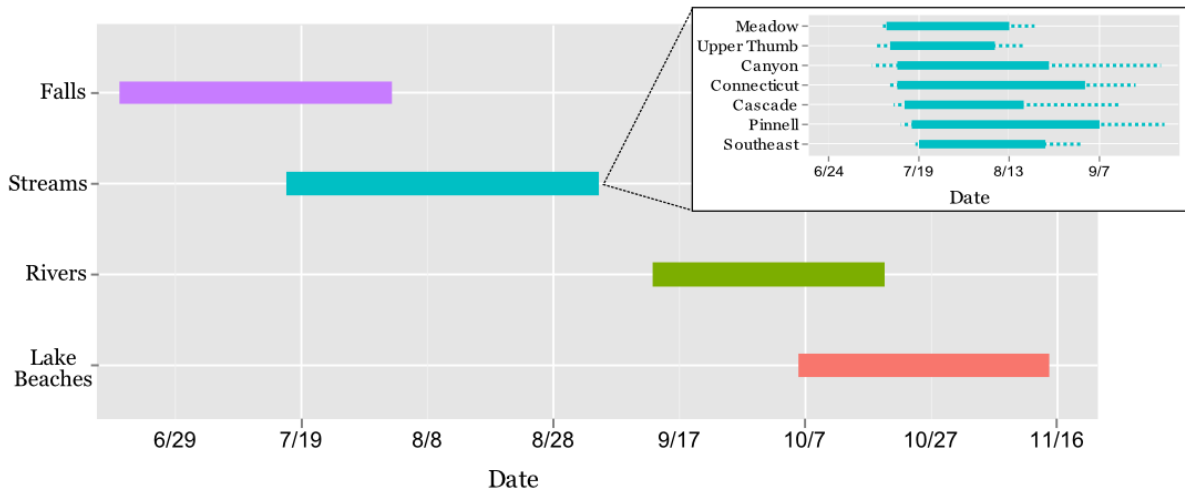
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## FIGURES

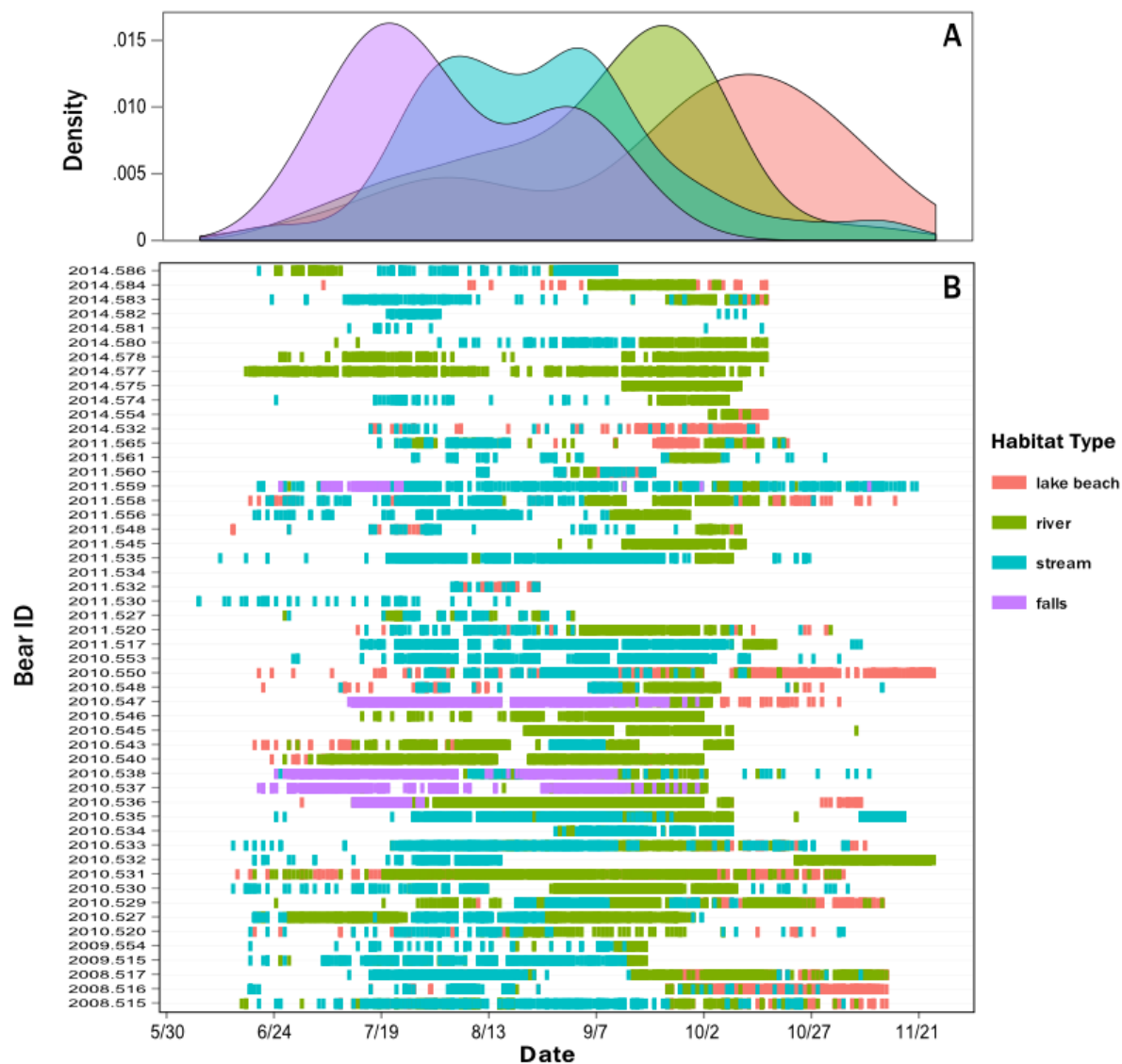
**Figure 1.1:** Map of study area on southwest Kodiak Island, Alaska, USA. There are 95 water bodies in this area used by spawning Pacific salmon (*Oncorhynchus* spp.). These sites are colored by habitat category, each of which corresponds with a different period of salmon availability to bears. Salmon availability in streams, rivers, and lakes occurs during salmon spawning while availability at falls occurs during salmon migration. All of these sites are assumed to be available to bears in the study area.



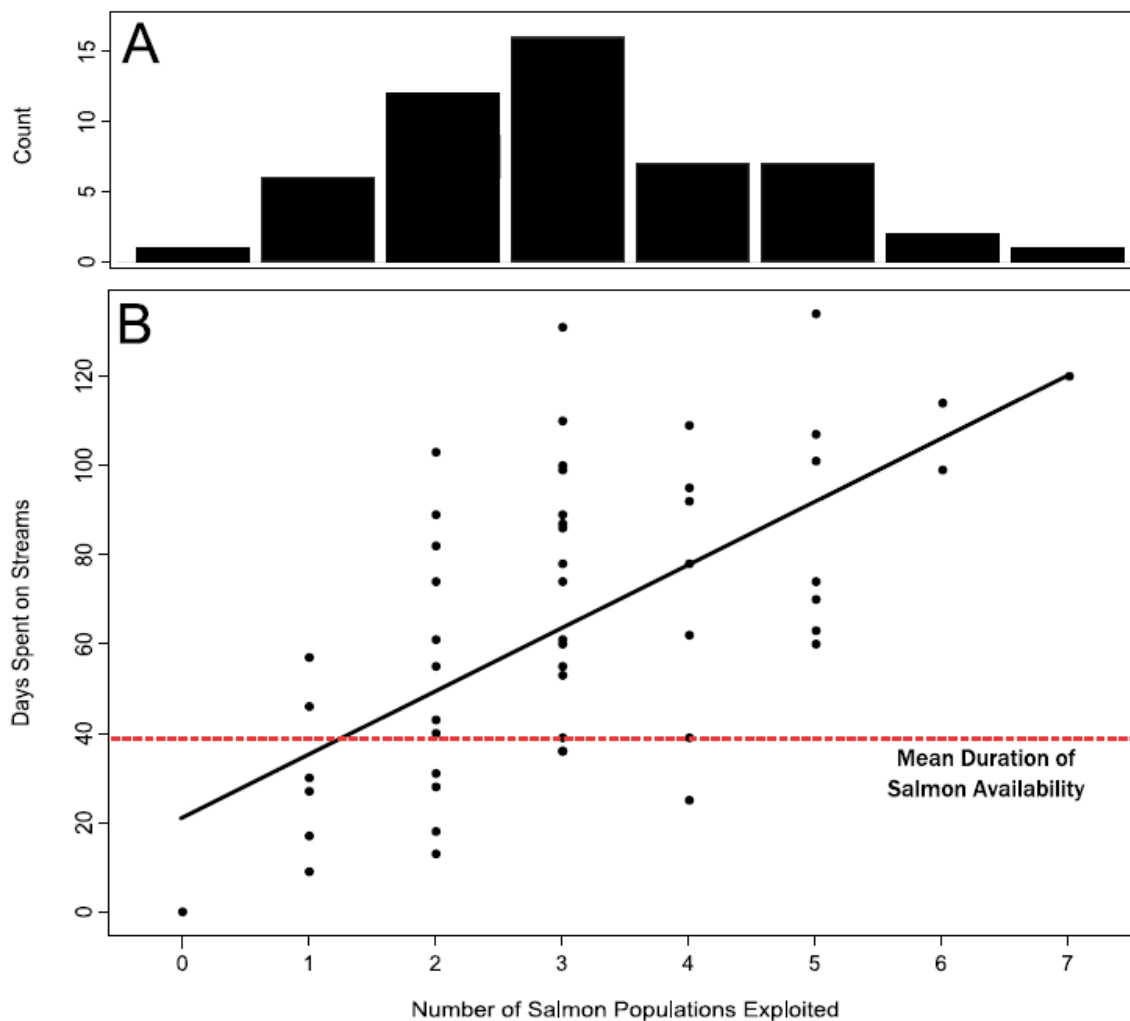
**Figure 1.2:** Dates of salmon availability in four aquatic habitats. Inset shows salmon spawning phenology of seven streams within the study area. Solid lines indicate periods with salmon in all years, while dotted lines indicate less frequent salmon observations. Salmon are available at a single site for an approximately 40 days while overall availability spans at least 150 days.



**Figure 1.3:** Seasonal use of salmon spawning/migration sites by GPS collared bears as a function of habitat type. A) Location data pooled across individuals and grouped by habitat type. Data were smoothed using a kernel density estimator with a bandwidth of 7.97, which was arbitrarily selected because it highlights the general pattern in bear habitat use (Silverman 1986). B) Individual timelines of bear use of salmon spawning/migration sites. Each row corresponds to a bear-year. Colors indicate habitat class attended each day, whereas the absence of any marker indicates periods where bears were not attending salmon sites.



**Figure 1.4:** (A) Histogram of the number of spawning populations exploited by GPS collared bears. Median = 3.0 populations. (B) Number of days collared female bears ate salmon as a function of the number of salmon populations exploited. Simple linear regression shown;  $P < 0.0001$ ,  $R^2 = 0.36$ . Red dashed line corresponds with the maximum length of time a bear could eat salmon if there was no phenological variation among salmon populations.



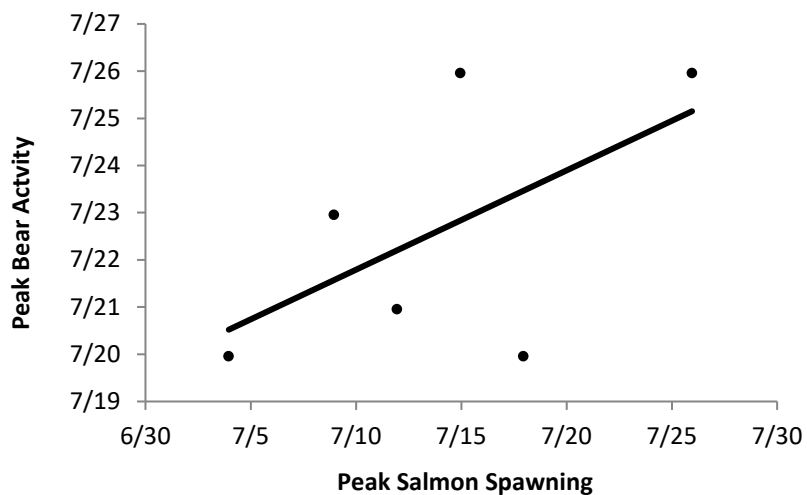


## APPENDICES

**Appendix A:** Sockeye salmon (*Oncorhynchus nerka*) entering Meadow Creek, a tributary to Karluk Lake, the largest of three lake systems in southwest Kodiak, Alaska. These lake systems have dozens of streams, rivers, and lake beaches used by salmon as spawning habitat. Shallow streams such as Meadow Creek leave salmon vulnerable to predators such as brown bears (*Ursus arctos middendorffi*). Photo credit: William Deacy.



**Appendix B:** The relationship between salmon spawning phenology and bear activity across 6 streams in 2012. Peak bear activity is defined as the median of the cumulative distribution function (CDF) of bear detections, whereas peak salmon is the date of highest observed abundance.  $R^2 = 0.3262$ .



**Appendix C:** Contingency table of habitats visited first and last by the 41 bears that visited at least 2 habitats.

|        | Visited First | Visited Last |
|--------|---------------|--------------|
| Falls  | 5             | 0            |
| Stream | 25            | 5            |
| River  | 6             | 21           |
| Lake   | 5             | 15           |



## CHAPTER 2

### TRAVEL-SPECIFIC RESOURCE SELECTION BY FEMALE KODIAK BROWN BEARS DURING THE SOCKEYE SALMON SPAWNING SEASON

#### ABSTRACT

Access to salmon resources is vital to coastal brown bear (*Ursus arctos*) populations. Deciphering patterns of travel allowing coastal brown bears to exploit salmon resources dispersed across the landscape is critical to understanding their behavioral ecology, maintaining landscape connectivity for the species, and developing conservation strategies. We modeled travel behavior of 51 radio-collared female Kodiak brown bears (*U. a. middendorffi*) from 2008 to 2015 during the sockeye salmon (*Oncorhynchus nerka*) stream spawning season to identify landscape patterns associated with travel pathways. To accomplish this, we identified the behavioral state of travel for radio-collared individuals, identified informative explanatory variables to include in analyses, and developed resource selection models at two spatial scales to evaluate environmental covariates that were effective predictors of travel behaviors. The models enabled spatial predictions of the relative probability of selection while bears were travelling and identified areas that contained potential movement corridors important for bears inhabiting Kodiak Island. At the study area scale landcover edges, elderberry-salmonberry stands, elevation, and stream length strongly influenced selection for travel corridors. For fine-scale selection local habitat diversity, water edge, and lowland bare, meadow, and tree landcovers strongly influenced selection while traveling. Our results present a novel framework to characterize factors influencing travel, identify important movement corridors, and provide managers with information to make informed resource management decisions.

## INTRODUCTION

Understanding how animals move through landscapes to exploit heterogeneously distributed resources is critical for their conservation and management, especially as human development and environmental change potentially disrupt animal movements and landscape connectivity. The ability of an animal to traverse the landscape to access resources and their decisions affecting movement patterns have implications for individual fitness and conservation of populations. These decisions and the factors driving consequent space-use patterns have fitness and management implications (Myserud et al. 2001; Wang et al. 2006; Hebblewhite et al. 2008; Ruff et al. 2011). Resource selection studies, which have emerged as a primary tool for understanding animal space use, commonly compare the locations used by wildlife with locations assumed to be available. Recent advances in resource selection methods have facilitated investigations not only at a home range scale, but also at finer spatial and temporal scales (Squires et al. 2013; Thurfjell et al. 2014; Edelhoff et al. 2016; Zeller et al. 2016; Gese et al. 2018; Osipova et al. 2018; Patin et al. 2020; Clontz et al. 2021).

Movement patterns and factors that influence these patterns often vary across seasons and animal behavioral states because animals move deliberately within the landscape depending on their current needs, aims, and the distribution of resources (Wilson et al. 2012; Thurfjell et al. 2014; Zeller et al. 2014; Patin et al. 2020; Ellington et al. 2020). Patterns of resource selection depend on an animal's behavioral state and the motivations and objectives specific to those behavioral states. Resource needs often vary a great deal among behavioral states and seasons (Beyer et al. 2010; Wilson et al. 2012; Roever et al. 2014; Clontz et al. 2021). For example, selecting sites for rest or avoiding risk likely involves a selection of environmental characteristics different from those for foraging or travel. With a few notable

exceptions, most studies have not discriminated among behaviors that might drive different patterns of resource selection. These studies provide insights into general patterns of space use, but not behavior-specific patterns. Ignoring behavioral states may limit our ability to better understand a species' movement ecology and functional landscape connectivity (Roever et al. 2014).

A challenge in the effort to understand how habitat selection varies with behavior has been how to accurately identify behaviors from animal location data. A number of recent studies have attempted to address this. Sorum (2013) carried out an innovative investigation of seasonal diets of Kodiak brown bears (*Ursus arctos middendorffi*) by using a combination of activity data and patterns of GPS locations to identify recent bedding sites (resting behavior) where they collected scat for seasonal diet analyses and also examined factors that influenced selection of bedding sites. Several studies have employed hidden Markov modeling (HMMs) approaches to analyze radio-telemetry locations to differentiate behavioral states (Abrahms et al. 2016; Karelus et al. 2019; Clontz et al. 2021). Using HMMs, Franke et al. (2004) successfully identified bedding, feeding, and travel behavioral states of woodland caribou (*Rangifer tarandus*). In a study of African wild dogs Abrahms et al. (2016) demonstrated that aggregating all movement data in the analysis (i.e., failing to take into account behavior-specific resource use patterns) can lead to misleading interpretations. Clontz et al. (2021) used HMMs to analyze movement patterns and identify associated behaviors (resting, foraging, and travelling) of wild pigs (*Sus scrofa*) in the Savannah River valley near the Georgia-South Carolina border to then develop behavior-specific resource selection models according to season. Wild pigs selected for different landscape attributes depending on their behavioral state. Hance et al. (2021) used GPS collar

and accelerometer data and an HMM to successfully differentiate movement and resting behaviors to identify resting sites for fishers (*Pekania pennant*) in Oregon and California. Karelus et al. (2019) carried out a study of black bears in which they used HMMs and Step Selection Functions (SSFs) to incorporate season, diel patterns, sex, and behavioral state to investigate habitat selection. They found that habitat selection varied with behavioral state.

Pohle et al. (2017) described the difficulties in using tracking data to identify a biologically meaningful number of behavioral states when using HMM. They provided suggestions on steps to remedy this and illustrated their approach with a case study of a single adult female muskox (*Ovibos moschatus*). Both Pohle et al. (2017) and Edelhoff et al. (2016) emphasized that too strict a focus on statistical procedures to identify behavioral states can lead to models with superior goodness of fit that cannot be linked to biologically meaningful or interpretable behaviors, and that the complexity of HHMs makes them challenging to apply to empirical data.

Patin et al. (2020) offered an effective alternative to HMM through a segmentation-clustering approach based on bivariate time series of location data for identifying behavioral states that can then be confidently related to environmental factors. Patin et al. (2020) stated that HMMs require the user to identify initial state-dependent probability distribution parameters, whereas their segmentation-clustering approach does not require such a precondition. Their methods not only rivaled that of HMM-based approaches, but even outperformed them in some cases.

A number of studies have investigated landscape patterns that foster or impede travel behavior for wildlife (Abrahms 2016; Monteith et al. 2018; Osipova et al. 2018). A model of a proposed road across the Serengeti revealed that it would adversely impact wildebeest

movement and access to seasonally available forage resources causing a 33% decrease in the population (Holdo et al., 2011). An investigation of migratory patterns of mule deer (*Odocoileus hemionus*) and the effects of energy development in Wyoming documented the importance of access to seasonal travel pathways enabling mule deer to access critical forage resources (Monteith et al. 2018).

Movement behavior for bears can be classified into three biologically meaningful states: resting, foraging, and travel or transit (Patin et al. 2020; Clontz et al. 2021). These states can be characterized using GPS location data based on derived estimates of speed and tortuosity, (Zeller et al. 2014; Edelhoff et al. 2016; Gurarie et al. 2016; Patin et al. 2020). For example, resting behavior is characterized by little movement and low activity. Foraging behavior is indicated by high tortuosity and low speed. Transit or travel behavior is characterized by low tortuosity and higher speed (Patin et al. 2020).

Numerous studies have emphasized the importance of salmon resources to coastal brown bears (*Ursus arctos*; Barnes 1990; Hilderbrand et al. 1999; Ben-David et al. 2004; Gende and Quinn 2004; Schindler et al. 2013; Hilderbrand et al. 2019; Mangipane et al. 2020; Rogers et al. 2020). Van Daele et al. (2013) quantified the consumption of salmon by Kodiak brown bears, emphasizing the importance of ecosystem based management of salmon escapement to maintain the dense bear populations found on the Kodiak Archipelago. Recent research has established that Kodiak brown bears prolong their access to spawning sockeye salmon (*Oncorhynchus nerka*) by exploiting variation in spawning phenology across the landscape (Deacy et al. 2016; Deacy et al 2018; Deacy et al. 2019). However, there is a lack of understanding of the habitat connectivity required to allow bears to move among salmon foraging sites.

A more thorough understanding of patterns of brown bear movement across the landscape to meet resource needs and the environmental features affecting these patterns is essential for a meaningful interpretation of habitat selection and for effective conservation and management efforts (Michelot et al. 2018; Karelus et al. 2019; Abrahms et al. 2020). Maintaining connectivity among important resources scattered across the landscape is critical for these conservation efforts (Clark et al. 2015; Panzacchi et al. 2016; Almasieh et al. 2019). Fecundity, body size, and population density of coastal brown bears are strongly correlated with salmon consumption (Hilderbrand et al. 1999; van Daele et al. 2013). Deacy et al. (2018) found that the ability of Kodiak Island brown bears to track and exploit a suite of salmon spawning habitats spread across the landscape, both temporally and spatially, had a greater effect on the amount of salmon in the diet than interannual variation in salmon abundance.

However, no studies to date have investigated the patterns of travel across the landscape by Kodiak brown bears to meet their resource needs. This is particularly important for travel during the salmon spawning season. Human actions that could hinder the ability of bears to travel freely across the landscape to access these streams and/or a reduction in the phenological diversity of salmon populations could adversely impact the bear population. Therefore, it is important to not only employ salmon management practices that maintain these salmon subpopulations, but also to implement management practices that allow bears to move freely across the landscape to exploit these resources (Barnes 1990; Deacy et al 2016; Deacy et al 2019).

Our goal was to secure a better understand of travel patterns by Kodiak brown bears and the factors influencing these patterns during the sockeye salmon spawning season (1 July

through 21 August). Our specific objectives were to 1) identify the behavioral state of travel for GPS-collared female brown bears, 2) identify variables associated with travel corridors, 3) develop resource selection models for female brown bears at two spatial scales to evaluate environmental covariates that characterize travel behavior, and 4) identify travel corridors during the sockeye salmon stream spawning season.

## **METHODS**

### ***Study Area***

The study area encompasses the southwestern region of Kodiak National Wildlife Refuge that includes three primary salmon stream-lake systems (Karluk, Frazer, and Red), dozens of spawning tributaries and rivers, and a dense population of brown bears (~250 independent bears/1000 km<sup>2</sup>; Barnes et al. 1988; Figure 2.1). The region has a maritime climate characterized by cool temperatures, overcast skies, and heavy precipitation. The topography of southwestern Kodiak is composed of a series of long fjords, a mixture of steep mountains, broad and short steep river valleys, gently rolling terrain, and wetlands. A mixture of deciduous tree species grow along rivers and streams. Lower elevation mountain slopes are covered in alder (*Alnus crispa*), salmonberry (*Rubus spectabilis*), elderberry (*Sambucua racemosa*), and forb-graminoid meadows. Alpine and subalpine vegetation and barren areas are common at elevations above 760 m. Large areas of lowland heath and shrub-graminoid wetlands are common in the subdued rolling lowlands (Fleming and Spencer 2004). Human activity within the study area is limited and dominated by recreation, primarily hunting, sport fishing, and bear-viewing.

Each lake-stream system included in our study is somewhat unique. Karluk Lake is long (20 km) and relatively narrow (ranging from 1.4 km to 3.1 km wide) and has 11 tributaries, most of which are short and shallow and have spawning salmon runs during July and August. The exceptions are O'Malley and Thumb Creeks, which have relatively larger flows and drain larger valleys. Thumb Creek has sockeye salmon runs from July through August. Sockeye salmon transit through O'Malley Creek on their way to spawning grounds in Canyon and Falls Creeks during July and August. During September and October sockeye salmon spawn in O'Malley River. Karluk Lake is drained by the Karluk River, which is approximately 40 km long and flows into the ocean on the western side of the island near Karluk Village. Spawning sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) are available to bears in the upper 4.3 km of Karluk River during September and early October (Leacock et al. 2014). Sockeye salmon spawn on suitable shoals along the shore of Karluk Lake largely from September through November, but also to a lesser degree during July-August.

Frazer Lake is 14 km long and approximately 1.3 km wide, and has one primary tributary, Pinnell Creek. Dog Salmon Creek drains Frazer Lake and runs south approximately 14 km emptying into Olga Bay. The Frazer drainage is unique among the two other lake-river systems due to the fact that it supports an introduced sockeye salmon population. Brood stock sockeye salmon were introduced into Frazer Lake from the Red Lake and Karluk Lake drainages during 1951-1971 (Blackett, 1979). From 1956-1962 returning adults sockeye were backpacked around a waterfall approximately one km below the lake outlet that presented a barrier to salmon migration. In 1962 a fish ladder was constructed at the waterfalls (Frazer Fish Pass) allowing spawning salmon to pass the



waterfall and establish a self-sustaining population. This was improved during 1971 and 1972 by building a diversion weir to help guide returning salmon towards the ladder,

The third drainage consists of the Ayakulik River and the smallest of the three lakes, Red Lake. Red Lake is 6.4 km by 1.3 km and has two significant tributaries with sockeye salmon runs, Connecticut Creek and Southeast Creek. Red Lake is drained by Red Lake River (6.3 km long) flowing into the Ayakulik River which runs for 23 km to the ocean on the west side of the island. Salmon spawn in Southeast and Connecticut Creeks in July and August. Salmon transit through Red Lake River to Red Lake and Connecticut and Southeast Creeks during July and August and spawn in Red Lake River itself during September.

The Alaska Department of Fish and Game (ADF&G) monitors salmon escapement into each of these systems with fish weirs on the Karluk River, Ayakulik River, and Dog Salmon Creek and the Frazer Fish Pass. During the period 2006-2018 sockeye salmon returns to Karluk Lake averaged 481,000 (181,000 during the early run and 300,000 during the late run) ranging from 53,000 in 2009 to 295,000 in 2007; Frazer Lake averaged 139,000 and ranging from 90,000 in 2006 to 219,000 in 2015; and Ayakulik/Red Lake averaged 163,000 ranging from 59,000 in 2006 to 218,000 in 2015 (McKinley et al 2019).

Sturgeon River, in the far west of the study area, consists of two branches – the East Fork and the Main Stem. The Main Stem Sturgeon is approximately 35 kilometers long from the headwaters to the Sturgeon Lagoon. The East Fork Sturgeon is approximately 17 km from its headwaters to the Sturgeon Lagoon. Both branches have chum salmon (*Oncorhynchus keta*) runs roughly between mid-June through mid-July (Price 2001). Runs on the Sturgeon River have been monitored only intermittently by fixed-wing surveys since 2000, but observations during annual aerial bear surveys from 2006 to 2018 suggest a

substantial decrease in the size of salmon runs on both the Main Stem Sturgeon and East Fork Sturgeon.

### ***Capture and Monitoring***

We captured adult female brown bears in the SW region of Kodiak Island, Alaska. All bears were anesthetized via darting from helicopter using a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol<sup>®</sup>, Fort Dodge Laboratories, Fort Dodge, Iowa, USA) at a dose rate of 10-12 mg/kg (Taylor et al. 1989). Standard zoological measurements, weights, and age estimates were taken for each bear. Capture and handling procedures were approved by the Institutional Animal Care and Use Committees (ADFG ACUC 07-08, USFWS IACUC Permit 2012008, USFWS IACUC Permit 2012008 Renewal, and USFWS IACUC Permit 2015-001). We fitted each bear with a GPS radio collar (Telonics Model #TGW-3790) programmed to record a location every hour from 15 May through 15 November. Collars contained a UHF (ultrahigh frequency) radio transmitter and were downloaded using an airplane fitted with a UHF receiver. We screened GPS locations for accuracy, removing relocations with a positional dilution of precision (PDOP) greater than 10 (Lewis et al. 2007). We excluded bears from the analysis if their collars failed before acquiring at least 1500 relocations in a year. We selected bear locations restricted to the period 10 July through the end of August to coincide with the annual salmon run.

### ***Defining Bear Movement Behavior***

We modeled travel behavior of 51 radio-collared female Kodiak brown bears over 76 bear-years from 2008-2015 during the sockeye salmon stream spawning season to identify landscape patterns associated with travel pathways. To identify travel behavior versus

foraging and resting or stationary behavior of female brown bears for use in subsequent models, we used a segmentation clustering method with the *seglust2d* package in R (Patin et al. 2019). This approach followed a modified version of Lavielle's method (Lavielle 1999) to detect change points between behavioral states in a time series of GPS locations for each individual (Ducros et al. 2020, Patin et al. 2020). We used speed and relative turning angle between successive 1-hour re-locations to differentiate behavioral states. We considered three behavioral states, or clusters, in our models that we defined as resting, foraging, and travel (Table 2.1). The minimum number of locations for each segment,  $L_{min}$ , was set to 5 (Patin et al. 2019). As a validation of this clustering technique to identify behavioral states, we used the activity sensor data on board the radio-telemetry collars collected with each bear location. We used an analysis of variance to evaluate whether mean activity sensor values from the transmitters differed significantly from each behavioral state identified with the segmentation clustering method. Activity sensor values were log transformed to ensure that data fit a normal distribution. Locations identified as travel/transit were used in subsequent resource selection analyses (Figure 2.2).

### ***Environmental Covariates***

Using variables identified in subset models, we evaluated competing models using a multi-scale analysis approach to evaluate both seasonal home range and fine-scale resource selection within the study area (Table 2). These two approaches were inherently nested and allowed us to identify movement corridors for the population in the study area and habitats selected by individuals within identified corridors. We utilized a traditional resource selection function (RSF) at the seasonal home range scale of the population of radio-collared bears to evaluate resource selection of bears while traveling. We used a step selection

function (SSF) to evaluate fine-scale selection by bears for each year. Our models enabled spatial predictions of the relative probability of selection while bears were traveling and identified factors influencing bear movements across the landscape.

We explored a suite of potential environmental predictor variables for both the seasonal home range and fine-scale selection analyses, which included both landcover and topographic features. Landcover covariates were derived from Kodiak Land Cover Classification 30 m raster data (Fleming and Spencer 2007), for which we aggregated landcover into 13 classes from 63 classes based on bear functional ecology (Figure 2.2). For each scale of selection, we considered 10 of the 13 aggregated landcover classes including dense alder, elderberry/salmonberry, tree (alder/birch/cottonwood/spruce), tall willow, low willow, wetlands, meadows, lowland tundra, lowland bare, and freshwater. We excluded rock/snow, marine, and freshwater landcover classes. Each landcover class was created by binary reclassification such that values of 1 equaled the landcover class of interest and values of 0 equaled other landcover classes.

For each landcover class, we calculated an edge diversity metric. The edge diversity metric was calculated for each landcover class as the absolute difference between the mean value of each raster cell and the 8 cells surrounding the center cell. Edge diversity ranged from 0 (all 8 surrounding raster cells were the same landcover class as the center cell) to 0.89 (all 8 surrounding cells represented a different landcover class than the center cell), and represented landscape edge diversity at the local scale. Landscape edge diversity provides a measure of the amount of contrasting edges among landcover classes. In addition, we calculated a landscape uniqueness index that summed the number of unique landcover classes within the center cell and 8 surrounding cells (landscape uniqueness index values

ranged from 1 to 9). Uniqueness measured the local diversity around each location. A more diverse immediate landscape provides more immediately available resources including, but limited to, foods, cover, and escape terrain.

To further refine layers representing water and to more accurately define salmon streams, we merged the water landcover class with stream layers that were developed manually to create a comprehensive water covariate. Stream morphology was also evaluated for the study streams. To quantify the influence of stream morphology on bear habitat use, we measured stream depth, width, vegetation cover, and substrate size along the salmon-accessible length of each focal stream. A field crew walked each stream, recording these metrics at 5m increments along the stream. The upstream limit of spawning activity was obvious on several streams because there was a salmon impermeable barrier such as a waterfall or dense downed vegetation. On unobstructed streams we determined the upstream limit of spawning by surveying for evidence of past spawning activity by looking for sockeye jawbones, which tend to persist through winter, bear trails, and other bear sign. If no evidence of previous spawning activity was observed over 100 consecutive meters of stream, we discontinued the morphology survey. We used the shapefile generated from this effort and merged it with the water landcover layers creating the comprehensive water covariate/landcover class.

Covariates describing topography were derived from a 30-meter digital elevation model (DEM; US Geological Survey 2011). We calculated percent slope, roughness, terrain ruggedness index (TRI), and topographic position index (TPI) with the *raster* package in R (Hijmans 2020). Roughness was calculated as the difference between maximum and minimum elevation of the center cell and the 8 surrounding cells (Wilson et al. 2007). TRI is

a measure of local terrain variation and was calculated as the mean of the absolute difference between the elevation at the location/center cell and each of the 8 surrounding cells (Wilson et al. 2007). TPI is a method to identify the relative position of a point along a topographic gradient, i.e., along a ridge, mid-slope, or valley. TPI was calculated by comparing the elevation of each cell to the mean elevation of the 8 surrounding cells (Guisan et al. 1999). Positive TPI values correspond to ridges or hilltops, negative TPI values are indicative of topographic depressions within the surrounding landscape such as valleys, gullies, and mountain passes, and values approaching 0 are indicative of flatter topography and mid-slopes (Weiss 2000; Knitter et al. 2019).

### ***Resource Selection Analysis***

We estimated travel-specific resource selection functions (hereafter, RSFs) for female brown bears at the scale of the study area (described below) using binomial generalized mixed models with package *lme4* in R (Bates et al. 2015). We used an individual intercept term nested within year in the model to account for individual variation among years and possible variation in selection by individuals across years, as well as to address the issue of pseudo-replication within individuals (Gillies et al. 2006). To estimate available habitat, we manually digitized a polygon surrounding pooled travel locations of all bears and then buffered the all-bears polygon by the average movement distance between bear locations. We considered this the study area and randomly generated 10 available locations per bear-use location to represent available travel habitat across the study area. We extracted covariate values at each used and available location. For RSF models we calculated values of environmental covariates within a 275-meter radius circular buffer. This buffer represented half of the average distance traveled by female brown bears between relocations (described

below), and therefore buffered average values within 275 m are likely better representations of the environment at the scale of bear selection during travel (Smith et al. 2020). For landcover covariates, we calculated the proportion of each landcover class within the circular buffer. For edge diversity and topography predictors, we calculated the mean values within the circular analysis buffer. We centered and scaled variables to ensure model convergence prior to modelling (Becker et al. 1988). The RSF took the following form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$$

where  $w(x)$  was proportional to the probability of female brown bear selection, and  $\beta_1$  represented the coefficient describing selection strength for covariate  $x_1$ , and  $n$  represented the number of covariates in the model.

### ***Step Selection Analysis***

We used a step-selection function (hereafter, SSF) to evaluate selection by bears at a finer scale for each year (bear-year). To estimate the SSF, the subset of travelling locations were paired with 10 available locations, or endpoints, generated by sampling the step length and turning angle distribution from the population of bears (Fortin et al. 2005, Thurfjell et al. 2014, Signer et al. 2019). We extracted covariate values at each used and available endpoint for each step. We applied conditional logistic regression to compare characteristics of used to available locations, with each stratum consisting of a used point and 10 paired available points. We assigned each individual to a cluster to calculate standard errors and 95% confidence intervals, the equivalent of a random intercept per individual in this modeling context (Craiu et al. 2008) using the survival package in R (Therneau 2015). We estimated the SSF ( $w(x)$ ) with the following form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$$

where  $\beta_l$  represented the coefficient describing selection strength for covariate  $x_l$ , and  $n$  represented the number of covariates in the model.

### ***Model Selection and Validation***

For both RSF and SSF approaches, we used a variable sub-setting approach (Arnold 2010) to develop nested candidate models and determine the most parsimonious set of covariates to describe selection by travelling female brown bears during the salmon stream spawning season. We started by exploring all variable combinations within landcover, edge diversity, and topography variable groups separately. We did not allow variables in the same model when they were highly correlated ( $|r| > 0.75$ ) and set the maximum number of variables in any model at 4 to minimize any model overfitting. We retained variables in the most predictive models from each subset, and assessed all combinations of remaining variables, including the length of salmon stream covariate. We again ensured that correlated variables were not included in the same model and set the maximum number of variables in any model at 8 to avoid potential model overfitting. Candidate models were fit with package *MuMIn* in R (Barton 2020). We used Akaike's Information Criterion (AIC) to assess support for all models (Burnham and Anderson 2002) and considered models within 2 AIC of the best model to be competitive. If AIC scores were nearly equivalent (i.e., within 2 AIC), we evaluated support of individual covariates by evaluating whether coefficients had 95% confidence intervals that did not overlap zero (Burnham and Anderson 2002, Arnold 2010).

We used 5-fold cross validation to evaluate the most-supported RSF model by randomly partitioning data by individual bear-years. We estimated predictions based on 4 of the 5 groups (training data) and compared them to the withheld group, and repeated this until the 5 withheld groups were evaluated (Johnson et al. 2006). We binned predictions into 6



equal-area (quartile) intervals (Wiens et al. 2008). Validations were performed by running simple linear regression models on the number of observed locations from the test group compared to expected locations generated from each RSF bin (Johnson et al. 2006). We considered models to be good predictors when linear regression models had high coefficients of determination ( $r^2 > 0.9$ ) and 95% confidence intervals of slope estimates excluded zero and included 1 (Howlin et al. 2004). We mapped the most predictive RSF model and SSFs across the study area by using coefficients from the top model and distributed predictions into 6 equal area bins corresponding to increasing relative probability of selection.

## RESULTS

We used data from over 175,000 quality-checked GPS locations collected from 51 female brown bears with 76 unique bear-years spanning 2008-2015 (some bears carried collars for more than 1 year). We estimated a travel behavior RSF using 11,623 locations (mean, 153 locations per bear-year). We estimated the SSF using 9,501 locations (mean, 125 locations per bear-year). During the study period, bears moved an average of 550 m/h while engaged in travel behavior (95% CI: 501-598 m/h). The segmentation clustering method identified travel locations used for RSF and SSF models (Table 1). Visual inspection suggested that this method fit the data well and identified travel corridors that radio-marked female brown bears used on Kodiak Island (Figure 2.2). We found that activity sensor values recorded from radio-collars differed in concurrence with the behavioral states identified in the segmentation clustering method ( $F = 795.9$ ,  $P < 0.001$ ), providing additional justification for the use of the clustering approach.

### ***Resource Selection Analysis at the Home Range Scale***

While engaged in travel behavior, bears tended to select for landcover diversity (uniqueness), lowland bare landcover, topographic depressions, and edges. They tended to avoid elderberry-salmonberry, lowland tundra, lowland tundra edge, higher elevations, steep slopes, ridges and hilltops. The most predictive landcover covariate subset model for resource selection analyses at the seasonal home range scale included the covariates: landscape uniqueness, salmonberry-elderberry, lowland bare, and lowland tundra (Table 3). *Landscape uniqueness* was strongly selected for, lowland bare was weakly selected for, and *Elderberry-salmonberry* and *lowland tundra* were strongly avoided (Table 2.3; Figure 2.3).

Edges played a significant role in selection while engaged in travel behavior (Table 2). The best *Edge Diversity* subset model included lowland tundra edge, low willow edge, tree edge, and *water edge*. *Lowland tundra edge* was strongly avoided, and *Low willow edge*, *tree edge*, and *water edge* were strongly selected for (Table 2.3; Figure 2.3).

Topographic characteristics also influenced selection during travel behavior. The covariates *elevation*, *slope*, and *topographic position index* (TPI) produced the best *Topography* subset model (Table 2. 2). Higher elevations and steep slopes were selected against. Local knolls and ridges were avoided while valleys, gullies, and mountain passes were selected for during travel (Table 2.3; Figure 2.3).

We used these variables from the subset models to develop and test resource selection models at the seasonal home range scale. The RSF identified areas that favored travel across the study area that were not explicitly identified by the GPS-collared bears. Of the 10 candidate models we evaluated, the top model explaining brown bear selection while

traveling at the scale of study area, included the 8 predictor variables *elderberry-salmonberry*, *lowland tundra edge*, *low willow edge*, *tree edge*, *water edge*, *elevation*, *topographic position index* (TPI), and *stream length* (Table 2.4; Figure 2.6). This model was overwhelmingly more powerful than the other 9 models. The change in AIC from the top model to the next most informative model was 124.82 (Table 2.4). Female brown bears avoided *elderberry/salmonberry* and *lowland tundra edge* habitats while traveling (Table 2.5; Figure 2.3). Relative probability of selection decreased by approximately 30% when the proportion *elderberry/salmonberry* increased by 10%. Relative probability of selection decreased by approximately 93% as *lowland tundra edge* increased from zero to 0.33. Bears selected *low willow*, *tree*, and *water edge habitats*. Relative probability of selection increased by approximately 68%, 42%, and 77% as *low willow*, *tree*, and *water edges* increased from zero to 0.33, respectively (Figure 2.3). Variables describing topography in the final model included *elevation* and *TPI*. A 100 m decrease in elevation was predicted to increase relative probability of selection by approximately 19%. A 10% decrease in *TPI* was predicted to increase relative probability of selection by 7%. *Length of salmon stream* was positively correlated with female brown bear selection. A 100 m increase in length of stream within 275 m was predicted to increase relative probability of selection by 100% (Figure 2.3). The interpretation of change in relative selection probabilities per unit change in variables were calculated using unstandardized selection coefficients from the final model.

We partitioned the spatial predictions from the RSF to include only the highest 2 bins predicted values, which corresponded to the highest relative probability of selection, to highlight movement corridors (Figure 2.4). Areas with the highest predicted probability of selection were congruent with corridors identified by radio-marked bears (Figure 2.5), and

also identified other areas across the landscape that likely facilitate bear movements. The spatial prediction of the RSF was a good predictor of brown bear habitat selection while traveling. When we partitioned validation testing and training groups by individual bear, average  $r^2 = 0.94 \pm 0.01$  (SE), and confidence intervals of slope estimates included 1 and excluded zero in all folds (Table 2.7).

### ***Step Selection Analysis***

At the fine scale, bears strongly selected for lowland bare landcover and water edge and slightly less strongly for meadow, tree, and unique for travel. Bears weakly selected against elevation and roughness. The most informative *Landcover* subset model for the fine-scale analyses included the variables: *unique*, *lowland bare*, *meadow*, and *tree* (Table 2.7; Table 2.8 ). Each of these landcover types were selected for during travel. The *Edge Diversity* subset model included lowland bare, meadow, tree, and water edges, all positively associated with selection (Table 2.7; Table 2.8). The *Topography* subset model included elevation, roughness, and TPI, all weakly selected against (Table 2.7; Table 2.8).

The best model explaining brown bear selection while traveling, which included variables from all model subsets, contained 7 predictor variables (Table 2.9). Three models were within 2 AIC points of this model. These models were similar to the top model, but included one additional variable, so we interpreted the most predictive model. Female brown bears selected for lowland bare habitats, meadows, tree cover, and greater landscape uniqueness (Table 2.10 ). Bears were approximately 140%, 27%, and 26% more likely to select lowland bare, meadow, and tree cover during movements compared to other vegetation communities respectively. Relative probability of selection increased by approximately 23% for each unit increase (1 additional landcover type) in landscape uniqueness. Bears also

selected for water edge habitats. Relative probability of selection increased by approximately 64% as water edge index increased from 0 (no edge) to 0.33 (3 of 9 landscape pixels included water). Variables capturing topographic attributes in the model included elevation and roughness. A 100 m decrease in elevation was predicted to increase relative probability of selection by approximately 35%. A 10% decrease in roughness was predicted to increase relative probability of selection by 6%.

## **DISCUSSION**

Our work represents the first detailed analysis of travel behavior of Kodiak brown bears. We used travel behavior models based on GPS locations of female Kodiak bears to determine features associated with travel and identify travel corridors selected by bears during the stream sockeye spawning season in southwestern Kodiak. At the scale of the home range, our RSF analysis showed that bears select low elevation and relatively open terrain while travelling. At finer scales, our step-selection analysis showed that bears have strong selection for edges, where one habitat abuts another. In particular bears had very strong selection for the margins of lakes and rivers. These findings are consistent with the authors observations of bears in the wild: bear trails tend to follow the edges of disparate habitats, the edges of streams and lakes, and through concave terrain like mountain passes. This study characterized travel patterns and identified travel corridors across the southwestern region of Kodiak National Wildlife Refuge during the stream spawning salmon season.

We focused on GPS locations associated with travel behavior, rather than an aggregation of all behaviors or resting and feeding behavior. Consequently, habitat selection appeared to consistently reflect the relative ease or difficulty of moving through different habitats, rather than selection for feeding or resting sites. At the seasonal home range scale,

bears avoided traveling through elderberry-salmonberry stands, lowland tundra edge, higher elevations, and TPI. Though elderberry-salmonberry stands provide important food when in season (Sorum 2013; Deacy et al. 2017), salmonberry stands, in particular, are very dense and present relatively impenetrable obstructions for travel. Low values for TPI indicated that bears selected for valleys, low mountain passes, or similar topographic depressions for traveling within the landscape. Avoidance of lowland tundra edge may partly be an artifact of low levels of use of lowland tundra during the salmon season, largely due to the fact that most of the lowland tundra is in the west-southwest region of the study area, more distant from salmon streams and the fact that lowland tundra is largely covered by hummocks which makes travel difficult. This is a bit surprising because bear trails are often observed where willow and/or alder stands meet lowland tundra. Selection for low willow edge, tree edge, and water edge emphasizes the importance of edge habitat for travel. Edges along these different landcover types often offer narrow travel paths that are clear of obstructions and proximity to escape cover. Selection for stream length reflects the relative ease of travel alongside streams and rivers and the fact that bears often move along streams to exploit stretches with high salmon concentrations.

The final SSF model identified covariates that were strong predictors of within-corridor selection or avoidance by individuals while traveling, rather than the broad-scale selection patterns across the landscape identified by the RSF. At this finer scale, bears selected for lowland bare habitats, meadows, tree cover, water edge, and greater landscape uniqueness. Selection for meadows, tree cover, and landscape uniqueness makes sense because spawning streams are commonly bordered by a mosaic of landcover classes. Additionally, this mosaic offers escape cover given the oftentimes large concentrations of

bears and their need to avoid intraspecific conflict and risk. Selection for *Landscape uniqueness* indicated that bears are selecting for areas with greater local landcover diversity. Selection for lowland bare habitats, which includes beaches and river gravel bars, pose easy travel paths largely free of obstructions oftentimes near salmon streams or connecting salmon streams. Bears selected against higher elevations and roughness. This is probably due to bears' selection for easier and more rapid travel paths among salmon spawning habitat, which are at valley bottoms or along lake margins.

These modeling efforts highlight the importance of behavior-specific resource selection and connectivity across the landscape. Collectively, the results of this analysis presented a novel framework to accurately identify factors influencing bear travel during the salmon stream spawning season at two spatial scales and provide managers with information to make informed decisions to conserve bear connectivity during salmon season. Our results show that during a critical period of foraging, the stream spawning season, bears use relatively few paths to travel among foraging sites. Although we were unable to assess how flexibly bears can change their movement corridors in response to disruption, our findings suggest that bears depend on specific paths, which, if blocked by human activities, could prevent efficient travel and foraging by bears.

Maintaining the integrity of these travel corridors is critical to the conservation and management of the Kodiak brown bear. Deacy et al. (2016, 2018, 2019) highlighted the importance of spawning salmon resources spread across space and time. To achieve the management goals of maintaining a high population level and body size of Kodiak brown bears, ADF&G and the Kodiak NWR must take steps to ensure that travel is facilitated by identifying travel routes and maintaining the integrity of those routes. A key finding of this

research is that bears heavily use very few corridors during the salmon season (Figures 2.4, 2.5). In particular, lake edges are narrow corridors which could be easily blocked by development or just the presence of people (citation).

Kodiak brown bears are currently able to exploit salmon resources widely spread across the landscape. Increasing recreation and development within some key areas within the study area could impede this ability to move freely among important salmon foraging areas. Specifically, recreation activities and infrastructure in the study area and elsewhere on Kodiak Island are often concentrated along lake shores, streams, rivers, and ocean beaches. Bears are often seen in these locations, but because they are frequented by people, it has been unclear whether observer bias creates a false impression of bears preference for these habitats (Leacock et al. 2014). In this study, we confirmed that bears indeed preferentially travel along lakeshores, streams, rivers, and ocean beaches, which sets up a potential conflict between human activities and bear conservation. These travel corridors must be managed carefully to prevent increasing human activities on the Refuge from hindering bear movements among critical resources, which allow Kodiak bear populations to achieve some of the highest densities and largest sizes on earth. Future studies investigating selection across all three behavioral states (resting, foraging, and travel), across all seasons, and among different classes of bears would add greatly to our understanding of the spatial ecology of coastal brown bears and allow agencies to better manage these populations and the lands they depend on.



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## TABLES

*Table 2.1:* Step Length and Turning Angle for Three Behavioral States.

| <b>Behavior</b> | <b>Step length (m)</b> | <b>Turning angles</b> |
|-----------------|------------------------|-----------------------|
| Stationary      | 76.4 (1.6)             | 180.8 (1.2)           |
| Foraging        | 199.7 (2.6)            | 179.5 (0.8)           |
| Travelling      | 588.6 (6.5)            | 180.3 (1.1)           |



**Table 2.2:** Top 10 candidate models within each variable subset group used to identify variables for subsequent evaluation of resource selection by female Kodiak brown bears while traveling. Variables in the top model for each variable subset were retained for final model selection.

| Model  | Model fit statistics <sup>a</sup> |              |                      |
|--|-----------------------------------|--------------|----------------------|
|  | <i>K</i>                          | $\Delta$ AIC | <i>w<sub>i</sub></i> |
| <b><i>Landcover</i></b>  |                                   |              |                      |
| Unique + Elderberry Salmonberry + Lowland bare + Lowland tundra                  | 5                                 | 0.00         | 1.00                 |
| Unique + Elderberry Salmonberry + Lowland tundra + Meadows                       | 5                                 | 516.22       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra + Low willow + Tree                      | 5                                 | 531.89       | 0.00                 |
| Unique + Elderberry Salmonberry + Low willow + Tree                              | 5                                 | 567.51       | 0.00                 |
| Unique + Elderberry Salmonberry + Low willow + Meadows                           | 5                                 | 586.95       | 0.00                 |
| Elderberry Salmonberry + Lowland bare + Lowland tundra + Low willow              | 5                                 | 640.87       | 0.00                 |
| Elderberry Salmonberry + Lowland bare + Lowland tundra + Low willow              | 5                                 | 675.62       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra + Low willow + Meadows                   | 5                                 | 799.98       | 0.00                 |
| Dense alder + Elderberry Salmonberry + Low willow + Tree                         | 5                                 | 801.82       | 0.00                 |
| Elderberry Salmonberry + Low willow + Meadows + Tree                             | 5                                 | 834.21       | 0.00                 |
| <b><i>Edge Diversity</i></b>   |                                   |              |                      |
| Lowland tundra edge + Low willow edge + Tree edge + Water edge                   | 5                                 | 0.00         | 1.00                 |
| Lowland bare edge + Lowland tundra edge + Low willow edge + Water edge           | 5                                 | 754.23       | 0.00                 |
| Elderberry Salmonberry edge + Lowland tundra edge + Low willow edge + Water edge | 5                                 | 955.10       | 0.00                 |
| Lowland bare edge + Low willow edge + Tree edge + Water edge                     | 5                                 | 982.65       | 0.00                 |
| Lowland tundra edge + Low willow edge + Tall willow edge + Water edge            | 5                                 | 1030.00      | 0.00                 |
| Elderberry Salmonberry edge + Low willow edge + Tree edge + Water edge           | 5                                 | 1063.18      | 0.00                 |
| Dense alder edge + Lowland tundra edge + Low willow edge + Water edge            | 5                                 | 1242.37      | 0.00                 |
| Lowland tundra edge + Low willow edge + Meadow edge + Water edge                 | 5                                 | 1357.18      | 0.00                 |

Table 2.2: cont'd

| Model   | Model fit statistics <sup>a</sup> |              |                      |
|---|-----------------------------------|--------------|----------------------|
|   | <i>K</i>                          | $\Delta$ AIC | <i>w<sub>i</sub></i> |
| Lowland tundra edge + Low willow edge + Water edge                            | 4                                 | 1404.87      | 0.00                 |
| Elderberry Salmonberry edge + Lowland bare edge + Low willow edge + Tree edge | 5                                 | 1418.98      | 0.00                 |
| <b>Topography</b>   |                                   |              |                      |
| Elevation + Slope + TPI   | 4                                 | 0.00         | 1.00                 |
| Slope + TPI   | 3                                 | 13.21        | 0.00                 |
| Elevation + TPI + TRI   | 4                                 | 100.60       | 0.00                 |
| TPI + TRI   | 3                                 | 122.87       | 0.00                 |
| Elevation + Roughness + TPI   | 4                                 | 135.82       | 0.00                 |
| Roughness + TPI   | 3                                 | 162.51       | 0.00                 |
| Elevation + Slope   | 3                                 | 925.97       | 0.00                 |
| Elevation + TRI   | 3                                 | 993.61       | 0.00                 |
| Elevation + Roughness   | 3                                 | 1026.94      | 0.00                 |
| Slope   | 2                                 | 1031.58      | 0.00                 |

<sup>a</sup>Number of parameters (*K*), change in Akaike's Information Criterion score from the top model ( $\Delta$ AIC) and Akaike weights (*w<sub>i</sub>*).

Table 2.3. Parameter estimates, standard errors (SE) and 95% confidence intervals for predictor variables from the most parsimonious model in each variable subset group describing resource selection by female Kodiak brown bears while traveling.

| Parameter             | 95% CI   |      |       |       |
|-----------------------|----------|------|-------|-------|
|                       | Estimate | SE   | Lower | Upper |
| <b>Landcover</b>      |          |      |       |       |
| Unique                | 0.45     | 0.01 | 0.43  | 0.47  |
| Elderberry            | -0.80    | 0.02 | -0.84 | -0.75 |
| Lowland bare          | 0.10     | 0.01 | 0.09  | 0.11  |
| Lowland tundra        | -0.73    | 0.02 | -0.77 | -0.69 |
| <b>Edge diversity</b> |          |      |       |       |
| Lowland tundra edge   | -0.65    | 0.02 | -0.68 | -0.62 |
| Low willow edge       | 0.48     | 0.01 | 0.46  | 0.50  |
| Tree edge             | 0.40     | 0.01 | 0.38  | 0.42  |
| Water edge            | 0.71     | 0.01 | 0.69  | 0.74  |
| <b>Topography</b>     |          |      |       |       |
| Elevation             | -0.07    | 0.02 | -0.10 | -0.03 |
| Slope                 | -0.61    | 0.02 | -0.65 | -0.58 |
| TPI                   | -0.44    | 0.01 | -0.47 | -0.41 |

**Table 2.4:** Top 10 candidate models evaluating resource selection for travel behavior of female brown bear at the seasonal home range scale. Variables assessed in candidate models were from variable subset models that were retained for final model selection.

| Model  | Model fit statistics <sup>a</sup> |              |                      |
|--|-----------------------------------|--------------|----------------------|
|  | <i>K</i>                          | $\Delta$ AIC | <i>w<sub>i</sub></i> |
| Elderberry Salmonberry + Lowland tundra edge + Low willow edge + Tree edge + Water edge + Elevation + TPI + Stream length    | 9                                 | 0.00         | 1.00                 |
| Elderberry Salmonberry + Unique + Lowland tundra edge + Low willow edge + Water edge + Elevation + TPI + Stream length       | 9                                 | 124.82       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra edge + Low willow edge + Water edge + Elevation + Slope + TPI + Stream length        | 9                                 | 156.38       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra edge + Low willow edge + Water edge + Elevation + TPI + Stream length                | 8                                 | 162.55       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra edge + Low willow edge + Tree edge + Water edge + Elevation + Slope + Stream length  | 9                                 | 222.22       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra + Low willow edge + Tree edge + Water edge + Elevation + TPI + Stream length         | 9                                 | 226.66       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra edge + Low willow edge + Tree edge + Water edge + Elevation + Stream length          | 8                                 | 242.36       | 0.00                 |
| Elderberry Salmonberry + Unique + Lowland tundra edge + Low willow edge + Tree edge + Water edge + Elevation + Stream length | 9                                 | 244.36       | 0.00                 |
| Elderberry Salmonberry + Lowland tundra edge + Low willow edge + Tree edge + Water edge + Slope + TPI + Stream length        | 9                                 | 276.35       | 0.00                 |
| Elderberry Salmonberry + Lowland Tundra + Low willow edge + Water edge + Elevation + Slope + TPI + Stream length             | 9                                 | 375.21       | 0.00                 |

<sup>a</sup>Number of parameters (*K*), change in Akaike's Information Criterion score from the top model ( $\Delta$ AIC) and Akaike weights (*w<sub>i</sub>*).

**Table 2.5:** Parameter estimates, standard errors (SE) and 95% confidence intervals for predictor variables in most parsimonious model describing female Kodiak brown bear resource selection while traveling.

| Parameter              | Estimate | SE   | 95% CI |       |
|------------------------|----------|------|--------|-------|
|                        |          |      | Lower  | Upper |
| Elderberry/Salmonberry | -0.41    | 0.02 | -0.44  | -0.37 |
| Lowland tundra edge    | -0.63    | 0.02 | -0.67  | -0.60 |
| Low willow edge        | 0.32     | 0.01 | 0.31   | 0.34  |
| Tree edge              | 0.16     | 0.01 | 0.14   | 0.19  |
| Water edge             | 0.35     | 0.01 | 0.32   | 0.37  |
| Elevation              | -0.44    | 0.02 | -0.47  | -0.41 |
| TPI                    | -0.24    | 0.02 | -0.27  | -0.21 |
| Stream length          | 0.39     | 0.01 | 0.38   | 0.41  |

**Table 2.6:** Five-fold cross validation results from female brown bear resource selection models. We considered models good predictors of resource selection when they had a high coefficient of determination, and 95% confidence intervals (CI) surrounding slope estimates ( $B_1$ ) that excluded zero and included 1. RSF models were considered acceptable when slope estimates excluded both zero and 1.

| K | $r^2$ | $B_0$  | CI                | $B_1$ | CI           |
|---|-------|--------|-------------------|-------|--------------|
| 1 | 0.98  | -60.00 | (-159.82, 39.82)  | 1.18  | (0.94, 1.42) |
| 2 | 0.97  | -1.75  | (-88.04, 84.53)   | 1.01  | (0.77, 1.25) |
| 3 | 0.89  | -74.66 | (-238.21, 88.89)  | 1.38  | (0.71, 2.05) |
| 4 | 0.96  | 29.85  | (-71.65, 131.36)  | 0.91  | (0.65, 1.16) |
| 5 | 0.89  | -29.53 | (-212.79, 153.73) | 1.11  | (0.56, 1.65) |

**Table 2.7:** Top 10 candidate Step Selection Function models in each variable subset group used to identify variables for evaluation of female Kodiak brown bear fine scale-selection while traveling.

| Model  | Model fit statistics <sup>a</sup> |              |       |
|--|-----------------------------------|--------------|-------|
|  | <i>K</i>                          | $\Delta$ AIC | $w_i$ |
| <b><i>Landcover</i></b>  |                                   |              |       |
| Unique + Lowland bare + Meadows + Tree                                   | 4                                 | 0.00         | 0.63  |
| Unique + Lowland bare + Lowland tundra + Tree                            | 4                                 | 2.03         | 0.23  |
| Unique + Lowland bare + Elderberry Salmonberry + Tree                    | 4                                 | 3.13         | 0.13  |
| Unique + Lowland bare + Dense alder + Tree                               | 4                                 | 14.26        | 0.00  |
| Unique + Lowland bare + Tree   | 3                                 | 16.11        | 0.00  |
| Unique + Lowland bare + Elderberry Salmonberry + Lowland tundra          | 4                                 | 16.17        | 0.00  |
| Unique + Lowland bare + Low willow + Tree                                | 4                                 | 17.68        | 0.00  |
| Unique + Lowland bare + Tall willow + Tree                               | 4                                 | 17.95        | 0.00  |
| Unique + Lowland bare + Elderberry Salmonberry + Meadow                  | 4                                 | 28.08        | 0.00  |
| Unique + Lowland bare + Lowland tundra + Meadow                          | 4                                 | 31.57        | 0.00  |
| <b><i>Edge Diversity</i></b>   |                                   |              |       |
| Lowland bare edge + Meadow edge + Tree edge + Water edge                 | 4                                 | 0.00         | 1.00  |
| Dense alder edge + Lowland bare edge + Meadow edge + Water edge          | 4                                 | 86.21        | 0.00  |
| Lowland bare edge + Low willow edge + Meadow edge + Water edge           | 4                                 | 89.52        | 0.00  |
| Lowland bare edge + Low willow edge + Tree edge + Water edge             | 4                                 | 90.06        | 0.00  |
| Lowland bare edge + Tall willow edge + Tree edge + Water edge            | 4                                 | 102.77       | 0.00  |
| Lowland bare edge + Meadow edge + Tall willow edge + Water edge          | 4                                 | 103.24       | 0.00  |
| Lowland bare edge + Lowland tundra edge + Meadow edge + Water edge       | 4                                 | 106.70       | 0.00  |
| Lowland bare edge + Meadow edge + Water edge                             | 3                                 | 106.73       | 0.00  |
| Elderberry Salmonberry edge + Lowland bare edge + Tree edge + Water edge | 4                                 | 107.03       | 0.00  |
| Lowland bare edge + Tree edge + Water edge                               | 3                                 | 107.74       | 0.00  |

*Table 2.7: cont'd*

| <b>Topography</b>           |   |        |      |
|-----------------------------|---|--------|------|
| Elevation + Roughness + TPI | 3 | 0.00   | 0.64 |
| Elevation + Slope + TPI     | 3 | 2.25   | 0.21 |
| Elevation + Roughness       | 2 | 3.82   | 0.10 |
| Elevation + Slope           | 2 | 6.00   | 0.03 |
| Elevation + TPI + TRI       | 3 | 7.53   | 0.01 |
| Elevation + TRI             | 2 | 11.04  | 0.00 |
| Elevation + TPI             | 2 | 41.22  | 0.00 |
| Elevation                   | 1 | 42.18  | 0.00 |
| Roughness + TPI             | 2 | 442.94 | 0.00 |
| Slope + TPI                 | 2 | 444.90 | 0.00 |

<sup>a</sup>Number of parameters ( $K$ ), change in Akaike's Information Criterion score from the top model ( $\Delta AIC$ ) and Akaike weights ( $w_i$ ).

**Table 2.8:** Parameter estimates, standard errors (SE) and 95% confidence intervals for predictor variables from the most parsimonious model in each variable subset group describing female Kodiak brown bear fine scale-selection while traveling.

| Parameter             | 95% CI   |       |        |        |
|-----------------------|----------|-------|--------|--------|
|                       | Estimate | SE    | Lower  | Upper  |
| <b>Landcover</b>      |          |       |        |        |
| Unique                | 0.32     | 0.01  | 0.28   | 0.37   |
| Lowland bare          | 0.88     | 0.08  | 0.58   | 1.19   |
| Meadows               | 0.16     | 0.04  | 0.004  | 0.32   |
| Tree                  | 0.18     | 0.03  | 0.08   | 0.28   |
| <b>Edge diversity</b> |          |       |        |        |
| Lowland bare edge     | 1.45     | 0.13  | 0.80   | 2.09   |
| Meadow edge           | 0.63     | 0.06  | 0.46   | 0.79   |
| Tree edge             | 0.51     | 0.05  | 0.31   | 0.71   |
| Water edge            | 2.81     | 0.07  | 2.60   | 3.02   |
| <b>Topography</b>     |          |       |        |        |
| Elevation             | -0.003   | 0.001 | -0.004 | -0.002 |
| Roughness             | -0.01    | 0.001 | -0.02  | -0.001 |
| TPI                   | -0.03    | 0.01  | -0.07  | -0.001 |

**Table 2.9:** Top 10 candidate models evaluating female Kodiak brown bear fine scale-selection while traveling. Variables assessed in candidate models were from initial variable subset models retained for final model selection.

| Model   | Model fit statistics <sup>a</sup> |              |       |
|---|-----------------------------------|--------------|-------|
|   | <i>K</i>                          | $\Delta AIC$ | $w_i$ |
| Lowland bare + Meadow + Tree + Unique + Water edge + Elevation + Roughness                  | 7                                 | 0.00         | 0.32  |
| Lowland bare + Meadow + Tree + Unique + Meadow edge + Water edge + Elevation + Roughness    | 8                                 | 0.16         | 0.29  |
| Lowland bare + Meadow + Tree + Unique + Water edge + Elevation + Roughness + TPI            | 8                                 | 0.49         | 0.25  |
| Lowland bare + Meadow + Tree + Unique + Tree edge + Water edge + Elevation + Roughness      | 8                                 | 1.71         | 0.14  |
| Lowland bare + Tree + Unique + Meadow edge + Water edge + Elevation + Roughness             | 7                                 | 11.49        | 0.00  |
| Lowland bare + Tree + Unique + Meadow edge + Water edge + Elevation + Roughness             | 8                                 | 11.98        | 0.00  |
| Lowland bare + Tree + Unique + Meadow edge + Tree edge + Water edge + Elevation + Roughness | 8                                 | 13.18        | 0.00  |
| Lowland bare + Meadow + Tree + Unique + Meadow edge + Water edge + Elevation                | 7                                 | 17.68        | 0.00  |
| Lowland bare + Meadow + Tree + Unique + Water edge + Elevation                              | 6                                 | 17.73        | 0.00  |
| Lowland bare + Meadow + Tree + Unique + Meadow edge + Water edge + Elevation + TPI          | 8                                 | 19.06        | 0.00  |

<sup>a</sup>Number of parameters (*K*), change in Akaike's Information Criterion score from the top model ( $\Delta AIC$ ) and Akaike weights ( $w_i$ ).

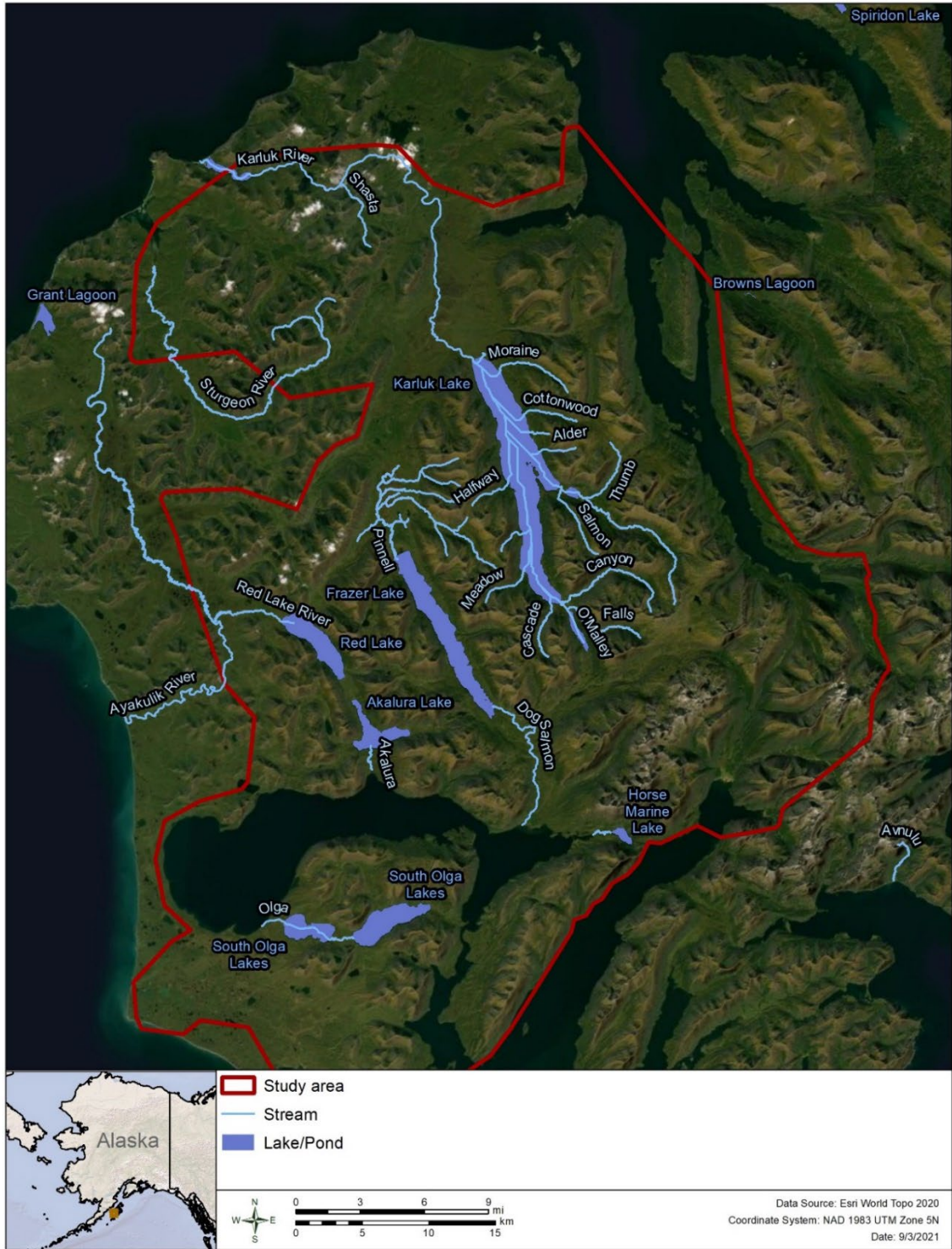
**Table 2.10:** Parameter estimates, standard errors (SE), and 95% confidence intervals for predictor variables describing female Kodiak brown bear fine scale-selection while traveling.

| Parameter    | 95% CI   |      |        |        |
|--------------|----------|------|--------|--------|
|              | Estimate | SE   | Lower  | Upper  |
| Lowland bare | 0.86     | 0.09 | 0.51   | 1.20   |
| Meadow       | 0.24     | 0.04 | 0.08   | 0.39   |
| Tree         | 0.23     | 0.03 | 0.13   | 0.32   |
| Unique       | 0.21     | 0.01 | 0.18   | 0.25   |
| Water edge   | 1.49     | 0.06 | 1.27   | 1.70   |
| Elevation    | -0.003   | 0.00 | -0.004 | -0.002 |
| Roughness    | -0.006   | 0.00 | -0.013 | 0.001  |



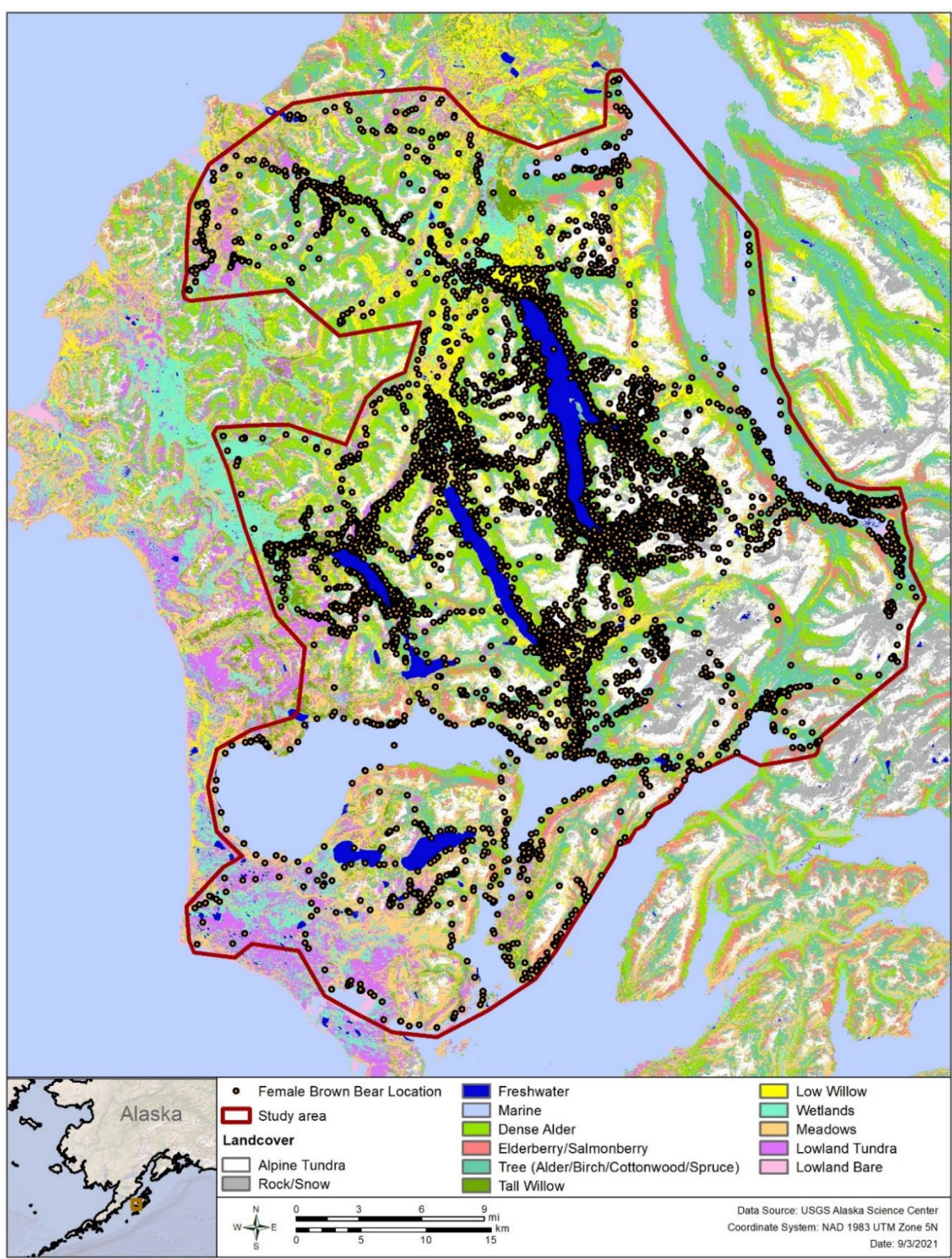
FIGURES

Figure 2.1: Kodiak Island, Alaska study area for Kodiak brown bear female movement during the salmon spawning season.

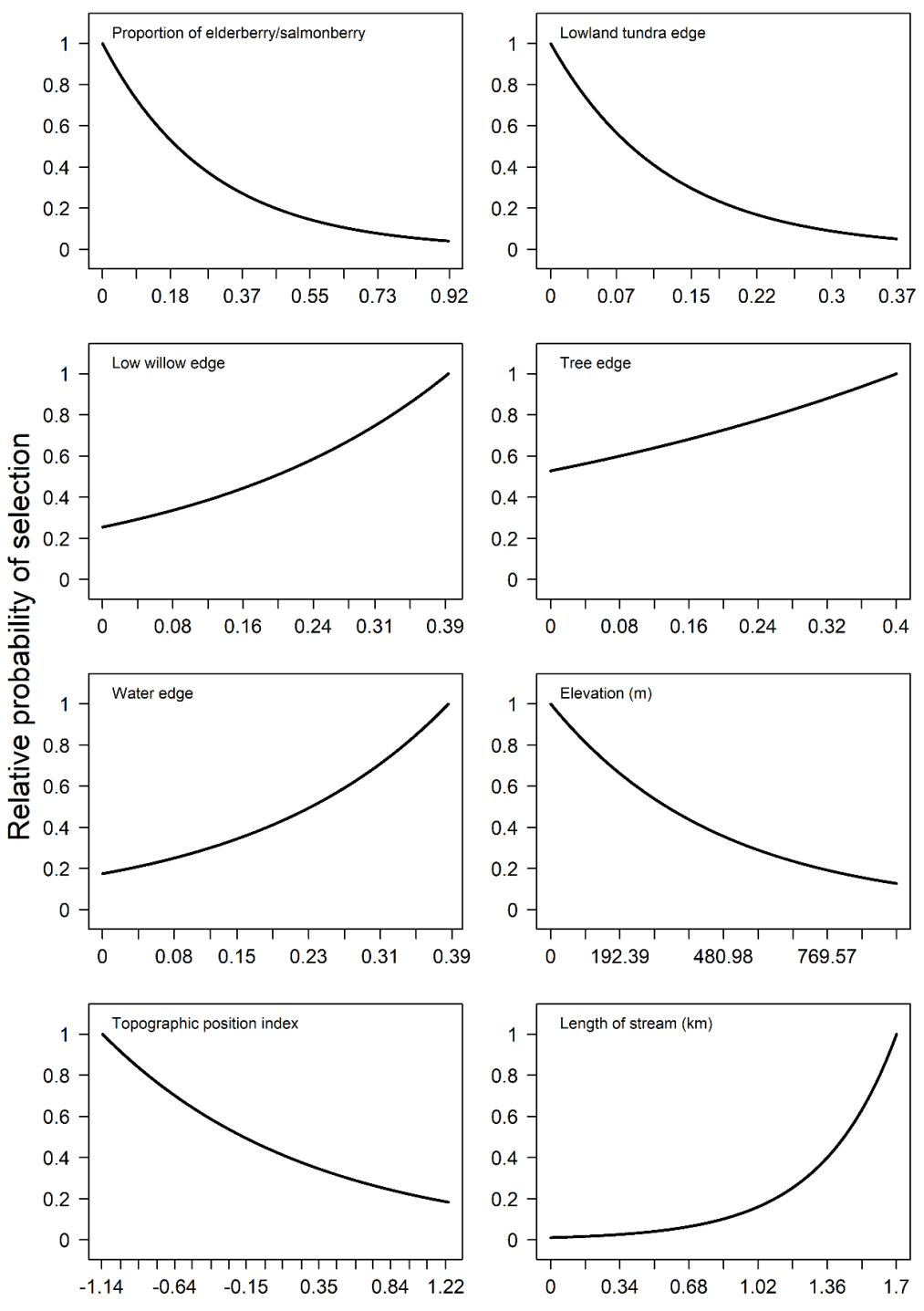




**Figure 2.2:** Locations of female brown bears associated with travel behavior identified during the salmon stream spawning season, 2008-2015 southwest Kodiak Island.

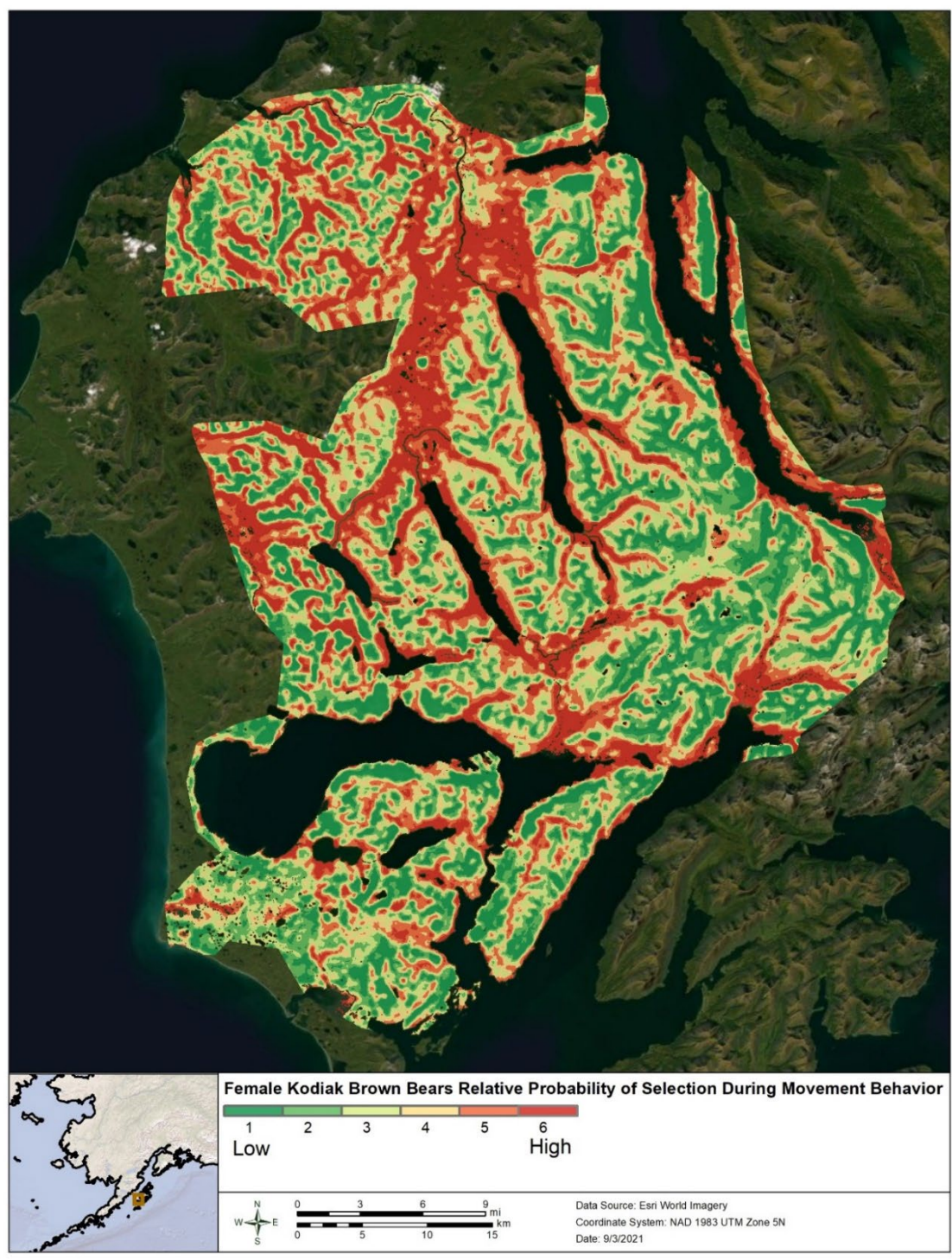


**Figure 2.3:** Relative probability of selection as a function of predictor variables in the most parsimonious model describing resource selection of female brown bears while traveling during the salmon spawning season on Kodiak Island.





**Figure 2.4:** Predicted relative probability of selection during travel by female brown bears during the salmon stream spawning season, 2008-2015 southwest Kodiak Island. Predictions were binned into 6 quantiles from low (bin 1) to high (bin 4) relative probability of selection.

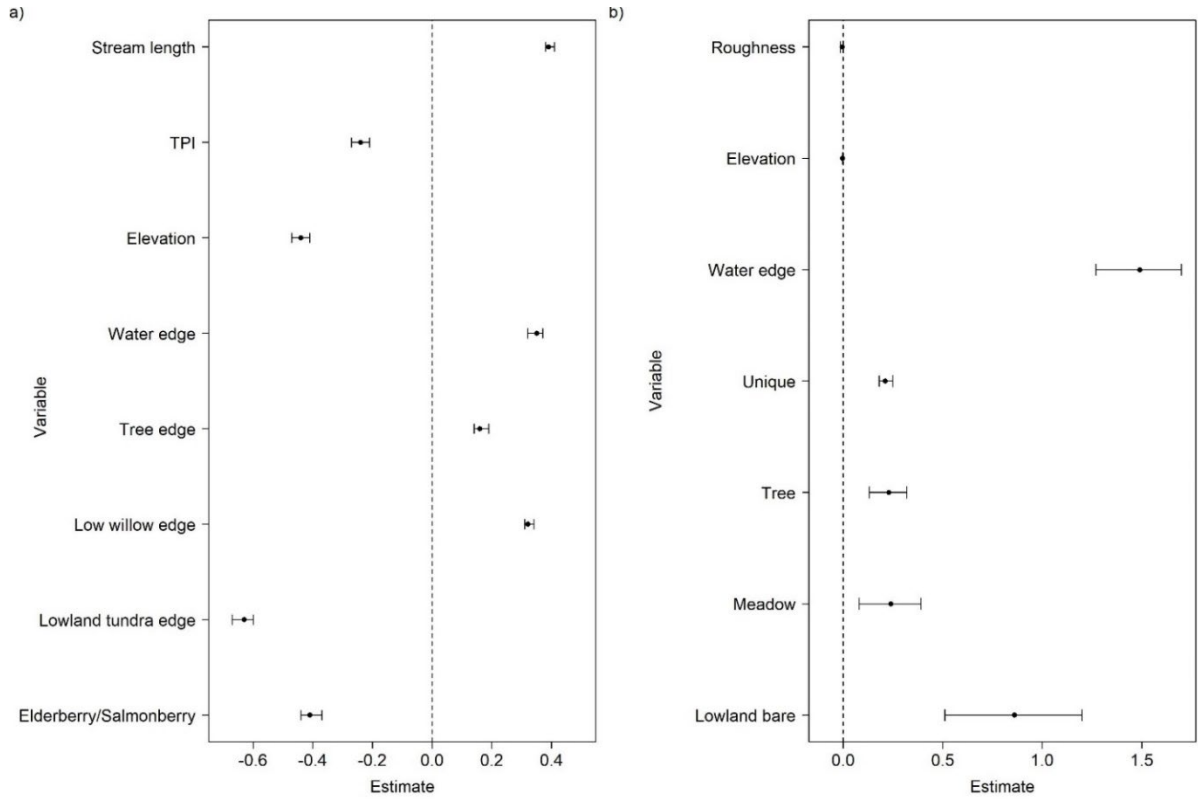




**Figure 2.5:** Intensity of female bear use of travel corridors during the salmon stream spawning season, 2008-2015 southwest Kodiak Island.



**Figure 2.6:** Parameter estimates with 95% confidence intervals evaluating resource selection of female brown bears on Kodiak Island while traveling at (a) home range scale and (b) patch-scales. Values below zero indicate avoidance, and values above zero indicate selection.



## CHAPTER 3

### VARIATION IN SPAWNING PHENOLOGY WITHIN SALMON POPULATIONS INFLUENCES LANDSCAPE-LEVEL PATTERNS OF BROWN BEAR ACTIVITY

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#### ABSTRACT

Animal consumers track spatial variation in resource phenology (i.e., resource waves) to prolong their access to ephemeral foods. While recent work has revealed how animals move across landscapes to exploit phenological variation among discrete foraging patches, much less is known about how variation nested within patches influences the spatiotemporal pattern of foraging opportunities and the behavior of consumers. Local, within-patch, variation in phenology influences levels of resource ephemerality and could dictate how frequently consumers must move to continuously exploit a pulsed food source. Here, we explore how within-site (stream) phenological variation relates to the duration of salmon (*Oncorhynchus nerka*) runs and its consequences for brown bear (*Ursus arctos middendorffi*) foraging behavior. We accurately quantified salmon run duration across a large number of spawning streams (21 site-year combinations). We found that salmon run duration varied threefold among spawning sites and that the source of prolonged runs was within-site variation in spawning phenology (i.e., the timing of arrival at spawning grounds). Although the estimated reproductive lifespan varied among sites, a simulation suggested that reproductive lifespan has little influence on salmon run duration. Salmon run duration strongly predicted the duration of site occupancy by bears, demonstrating that phenological

variation within salmon populations complements among-population variation to alleviate time constraints on salmon consumption. To explore whether within-population variation in salmon phenology was related to spatial variation in habitat conditions (as is the case with among-population phenological variation), we monitored water temperature, salmon availability, and bear activity across a longitudinal gradient in Connecticut Creek, the study stream with the most prolonged salmon run. Spawn timing varied spatially, occurring first in cold headwater reaches and later in warmer downstream reaches. Patterns of bear presence closely tracked this spawning sequence, suggesting they “surf salmon waves” not only across landscapes but also within spawning sites. However, a coarser analysis across multiple sites suggests phenological variation within salmon populations may not always be spatially structured. Our results demonstrate one way in which local variation in phenology can influence consumer foraging behavior, highlighting the need to understand the causes and consequences of phenological variation at multiple scales.

## **INTRODUCTION**

A key challenge for consumers is to meet energy demands when quality foraging opportunities are ephemeral (Wang et al. 2006, Yang et al. 2008, Armstrong and Schindler 2011). One way mobile consumers cope with ephemeral resources is by exploiting resource waves, which occur when spatial variation in resource phenology causes foraging opportunities to propagate across space and become less ephemeral at larger spatial scales (Armstrong et al. 2016). The resource wave concept has been used to describe the foraging opportunities of a range of different consumers (mostly birds, ungulates, and bears) with different dispersal abilities. There is strong evidence of animals tracking large-scale phenological variation (van Wijk et al. 2011, Deacy et al. 2016a, Aikens et al. 2017) at the



extent of animal home ranges or long-distance migration routes. However, phenology varies at multiple spatial scales and may exhibit a hierarchical structure, such that within- and among-patch variation exist together (Van Moorter et al. 2013). There is very little known about the existence and significance of smaller-scale phenological variation, for example, variation nested within the patches that animals move among while surfing known resource waves (but see Bronstein et al. 1990, Van Moorter et al. 2013). Fine-scale variation could mediate some of the costs associated with large-scale resource wave tracking by increasing the duration of quality foraging in a resource patch. Longer durations have the potential to benefit consumers by reducing the frequency and/or cumulative distance of movements among patches needed to surf a resource wave (move sequentially among patches with varying phenology), or by reducing the foraging penalty for foraging movement that are not perfectly timed with peaks in resource phenology. Here, we explore the relationship between within patch (i.e., a tributary stream) phenological variation in sockeye salmon (*Oncorhynchus nerka*) spawning and run duration, and how this influences the foraging behavior of Kodiak brown bears (*Ursus arctos middendorffi*).

Sockeye salmon tend to spawn at high densities for brief periods of time, presenting a pulse of resources for consumers (Gende et al. 2002). Water temperature is associated with sockeye salmon spawning phenology, and thermal heterogeneity is known to generate phenological variation at continental scales (Hodgson and Quinn 2002), in addition to finer scales, such as among spawning streams within a watershed (Taylor 1991, Lisi et al. 2013). This watershed scale variation has attracted recent interest because it generates resource waves at spatial extents that are within the movement capacities of important salmon consumers, such as bears. Indeed, recent studies have shown that brown bears move across

watersheds to consume sockeye salmon from multiple populations with varying spawning phenology (Figure 3.1; Schindler et al. 2013, Deacy et al. 2016a). It is clear among-site variation in spawning phenology is functionally important to consumers—by moving among several spawning sites where salmon are briefly available (~30 d), bears can consume salmon for much longer durations (up to 130 d). However, no research has examined the importance of within-site variation in spawning phenology, how it relates to spawning duration, and what this means for foraging consumers. This issue has important implications for food webs.

Within-site variation in salmon spawning could strongly mediate the flux of salmon subsidies to more sedentary consumers, such as sculpin and juvenile salmonids. For wide-ranging consumers like bears, both among- and within-site variation in phenology could influence the patterns of movement required for consumers to feed on salmon for extended periods (Figure 3.1). In theory, mobile consumers benefit most when a salmon portfolio (aggregate of salmon populations) has high within-site phenological variation (because this should increase spawning duration) and high among-site phenological variation (because this produces a resource wave; Figure 3.1).

The spawning duration at a single site (i.e., stream, lake beach, river) should be a function of two variables: how long salmon survive before senescing (i.e., their reproductive lifespan) and the length of time over which spawners arrive (i.e., within-site phenological variation). Reproductive lifespan can vary up to six fold among individuals (van Den Berghe and Gross 1986, Hendry et al. 2004) and is negatively correlated with arrival date (Carlson and Rich 2004, Hendry et al. 2004) and the risk of bear predation (Carlson et al. 2007). Variation in arrival date can emerge through heterogeneity in natural and sexual selection (Hendry and Day 2005). For example, access to ripe females can favor earlier arriving males,

while risks of nest disturbance (i.e., superimposition) can favor later arriving females (Dickerson et al. 2005). While it is well known that water temperature is strongly associated with variation in arrival dates among sockeye salmon spawning sites (Taylor 1991), there is surprisingly little known about whether this relationship exists within spawning sites. Methods for thermal mapping have improved greatly in recent years (Torgersen et al. 2012), allowing stream ecologists to better appreciate fine-scale patterning of water temperature (Torgersen et al. 1999, Steel et al. 2017). In coastal watersheds of Alaska, the range of temperatures expressed spatially within salmon spawning sites can encompass much of the total range in temperatures expressed across sites (Armstrong et al. 2013). However, because phenology is far more difficult to measure than temperature, how fine-scale thermal heterogeneity relates to salmon spawn timing is poorly understood. Quantifying site-level run duration requires intensive monitoring (i.e., daily-to-weekly surveys; Quinn and Gende 2003, Ruff et al. 2011, Davis 2015) that is logistically challenging when several sites are involved and requires levels of human activity that could displace bears and confound interpretations of bear behavior. Because of these challenges, few if any studies have characterized landscape-level variation in salmon run duration and we know of no studies that have reported how bear occupancy responds to such variation. This lack of research constrains our ability to understand the effects of salmon spawning phenology across spatial scales.

Prior research of brown bears on Kodiak Island, Alaska provided clues that variation in salmon run duration might be salient to bears that integrate across salmon populations. Brown bears that moved among salmon spawning sites (i.e., surfed the resource wave) could consume salmon for up to 130 d, yet there was substantial variation in how bears moved among spawning sites (Deacy et al. 2016a). Some bears (13%) used one or fewer spawning

sites and averaged only ~20 d of salmon consumption. This may be because of the availability of alternative resources (Deacy et al. 2017) or because movements come with risks (e.g., infanticide) that deter some individuals from fully capitalizing on resource waves (Ben-David et al. 2004). Further, some bears that exploited two or three salmon sites achieved as many days of foraging as bears that visited five to seven sites, suggesting some sites provided a more prolonged foraging opportunity. Here, we present results from a suite of tributary streams to (1) describe variation in the duration of salmon spawning; (2) test whether duration of salmon spawning is best explained by within-stream variation in spawning phenology or variation in reproductive lifespan; and (3) test whether the duration of bear presence is explained by the duration of salmon availability. In addition to these core objectives, we also (4) explored whether the longest duration site in our study exhibited thermal variation that resulted in longitudinal variation in salmon spawn timing and bear activity. Finally, we examine the evidence for bears tracking within-stream spatial variation in phenology across a wide spectrum of short and long duration sites.

## **METHODS**

### ***Study Area***

We conducted this work in southwest Kodiak Island, Alaska, an area with three primary salmon nursery lakes (Karluk, Frazer, and Red), dozens of spawning tributaries, and a dense population of brown bears (~250 individuals/ 1000 km<sup>2</sup>; Barnes et al. 1988). Generally, salmon are invulnerable to predation (due to deep water) until they arrive at spawning sites, such as tributary streams. To characterize among-site variation in spawning duration, we monitored salmon spawning in ten tributary streams from 2013 to 2015 (not all streams were monitored in all years; Figure 3.6, Table 3.1). To explore how bear presence

related to spawning duration, we monitored bear presence at seven of these streams during 2015.

### *Duration of Salmon Availability Among Spawning Sites*

We estimated spawning duration from time series of live fish abundance in each stream, using a time-lapse photography double sampling method paired with stream-specific estimates of reproductive lifespan (see below for details; Deacy et al. 2016b). This system consists of a time-lapse camera that takes photographs of the stream continuously and a video camera that records intermittently. These cameras recorded salmon moving upstream or downstream over white contrast panels secured to the streambed and infrared lights to allow detection of salmon at night. We estimated salmon passage by modeling the relationship between time-lapse salmon detections (which only record a fraction of the passing salmon) and video counts (which record nearly every passing salmon) with simple linear regression. The resulting regression was then used to estimate the passage of salmon for every hour of the spawning season. We estimated the daily salmon abundance as the total salmon that have entered the stream, minus those that have departed or have died. Salmon mortality was estimated with stream-specific mortality estimates. The double sampling method has been shown to estimate salmon abundance accurately (<10% error, Deacy et al. 2016b), and it allowed us to minimize displacement of bears due to human presence on streams. We calculated the duration of spawning by counting the number of days salmon abundance exceeded 10% of each stream's maximum salmon abundance. We used a threshold because the salmon abundance distribution generally has long tails during which few salmon are present. Because of this, the number of days above 10% abundance more accurately reflects

the period when bears can profitably forage on salmon than simply counting days where any salmon were present.

We estimated reproductive lifespan (RLS) in our streams with a linear model fit to existing morphology/RLS data (Carlson et al. 2007). Carlson et al. (2007) collected RLS data by tagging salmon prior to stream entry and then recording the number of days from stream entry to death. We compared models of RLS that included stream width or depth as predictors (we could not include both because they were strongly correlated) with AIC<sub>c</sub> (Akaike 1974). The model with depth best explained variation in RLS and had the equation,  $y = \text{depth (cm)} 9.0287 + 3.32$  (Deacy et al. 2016b). We collected morphology data in our study streams using established methods (Deacy et al. 2016b). Using an equation to predict mean RLS is not as robust as measuring it in situ. To test whether error in this parameter could cause error in estimated salmon run duration, we simulated salmon runs under two scenarios: (1) We fixed SD of stream entry date (SD = 12 d) while varying RLS from 2.25 to 22.35 d and; (2) we fixed RLS (7.9 d) while varying asynchrony in spawning dates (SD of stream entry date) across the range observed across the populations in this study (6–20 d). We selected a conservative range of mean RLS by starting with a range of mean RLS values (4.5–14.9 d) from a similar study area (Carlson et al. 2007). We then subtracted/added 50% to these minimum and maximum mean RLS values, respectively, to arrive at a range of 2.25–22.35 d. This range is conservatively broad to help ensure we simulated across the range of mean RLS values that could exist in our study system. In both simulations, we assumed that the standard deviation of RLS was proportional to the mean (SD = 0.499 x mean), as has been found in prior studies (Carlson et al. 2007). The output of each simulation was the

duration of salmon foraging, defined as the number of days where salmon abundance exceeded 10% of maximum salmon abundance.

We used least-squares linear regressions to compare the relative importance of estimated reproductive lifespan and within-stream variation in spawn timing (represented by the standard deviation of date salmon arrived in a spawning stream) on salmon run duration.

### ***Bear Tracking of Within-Stream Variation in Spawning Phenology***

Connecticut Creek has a uniquely long salmon run. To test whether the long duration of salmon spawning at Connecticut Creek was partially explained by spatial variation in spawning phenology, we deployed five time-lapse cameras (Day 6 Outdoors PlotWatcher Pro, Columbus, Georgia, USA) distributed evenly along Connecticut Creek from its mouth to its headwaters to detect salmon. The cameras were attached to stands (3.7 m Manfrotto Alu Master light stands, the Netherlands) adjacent to the stream and were aimed at the stream surface. The cameras were programmed to take a photograph every 30 min. To decrease the time required to code images, technicians did not count all salmon, but rather coded images as no salmon (value = 0), fewer than five salmon (value = 1), or more than five salmon (value = 2). We then summed the code values for each day as an indicator of the spatiotemporal pattern of salmon spawning.

We deployed nine time-lapse cameras (Reconyx RC55/PC800, Holmen, Wisconsin, USA, or Day 6 Outdoors PlotWatcher Pro, Columbus, Georgia, USA) along the length of Connecticut Creek to test whether bears responded to within-stream variation in spawning phenology. We distributed the cameras evenly from the mouth to a point upstream where we did not observe salmon during aerial surveys and found no evidence of past spawning during

ground surveys (e.g., jaws or gill plates). Cameras were deployed in June before the salmon run began and were removed in October, after spawning concluded. Cameras were programmed to take a photograph every five minutes during daylight hours. We counted the number of bears (excluding cubs) in each photograph and then summed counts by day. These counts do not census bears, but rather index overall bear use and have been corroborated by more direct monitoring techniques, including GPS telemetry (Deacy et al. 2016a). Although bears occasionally use streams for purposes other than foraging on salmon (e.g., travel corridor or water source), a prior study found that bears were detected by time-lapse cameras 61 times more frequently on streams when salmon were present compared to when salmon were absent (Deacy et al. 2016a). Thus, we feel confident in using time-lapse detections as a proxy for fishing activity. To account for differences among cameras (i.e., size of viewshed) and to focus on the phenology and duration of stream use, we converted all counts to cumulative distribution functions. We also deployed temperature sensors (Onset HOBO U22, Bourne, Massachusetts, USA) in the stream near each bear camera to assess whether variations in spawn timing were explained by differences in thermal regimes (Doctor et al. 2010). Sensors were anchored in the middle of the stream in a weighted housing and rested on the streambed. Temperatures were recorded hourly. We calculated the average temperature from July to February (the approximate months of egg incubation; Murray and McPhail 1988), because this is the period relevant to spawning salmon and incubating eggs.

### ***Bear Fishing Patterns at a Suite of Streams***

Cameras were deployed at nine additional streams (ten including Connecticut Creek). Because of logistical constraints, we deployed three cameras at each of stream (: Figure 3.6). We distributed the cameras evenly across the section of the stream in which salmon spawned



(generally from the stream mouth to an impassable barrier to fish, or to a point where we did not observe salmon during aerial surveys and found no evidence of past spawning [e.g., jaws or gill plates] during ground surveys). Cameras were placed in the same location with the same viewshed to ensure count effort was consistent across years. Cameras were deployed in late May or early June before salmon runs began and were removed in late August in 2013/2014 and late September in 2015, after spawning concluded. Cameras were programmed, and bears counted, as described above for Connecticut Creek.

We calculated bear foraging duration for each stream by pooling the time-lapse camera detections from all cameras on a stream and calculating the number of days between the 10th and 90th percentiles of the empirical cumulative distribution functions. This reduces the chance of confounding the analysis with bear detections that do not represent foraging because it excludes chance detections of bears passing by prior to and after salmon spawning runs.

Given the strong relationship between salmon spawning duration and bear fishing duration (Figure 3.2b), and the evidence that bears on Connecticut Creek exploited the within-stream resource wave (Figure 3.4d, we used bear responses on six additional streams to determine whether spatial variation in salmon phenology contributed to spawning duration at sites other than Connecticut Creek (we excluded Falls Creek because it had <50 bear detections). The validity of this approach relies on the assumption that bear foraging patterns reliably indicate salmon availability patterns, which is supported by observations made in prior studies that bears are rarely seen near streams when salmon are not present (Schindler et al. 2013, Deacy et al. 2016a).

## RESULTS

### *Salmon Spawning and Bear Fishing Duration*

The duration of sockeye salmon runs in ten headwater streams ranged from 22 to 72 d, with a median duration of 37.5 d (median of 2-yr stream averages, Figure 3.2a). Least-squares linear regression models indicated that population level run duration increased with within-stream variation (standard deviation) in the date of stream entry by salmon (year was not included in the most parsimonious model,  $P < 0.0001$ , Figure 3.2b), but not variation in mean estimated reproductive lifespan of spawning salmon ( $P = 0.62$ , Figure 3.2c). These results were corroborated by the results of a simulation of salmon run duration, which showed that across published ranges of reproductive lifespan and observed variation in arrival date, variation in arrival date tends to be much more influential (Figure 3.3). The duration of bear presence at ten streams ranged from 18 to 52 d with a median duration of 35 d. A linear regression model with a random intercept for year indicated that bear duration at streams increased with within-stream variation in arrival date ( $\chi^2(1) = 9.45$ ,  $P = 0.002$ , Figure 3.2d).

### *Salmon Spawning Pattern in Connecticut Creek*

Among the study streams, Connecticut Creek had the longest salmon run duration (average of 70.5 d,  $n = 2$  yr, Figure 3.2a). We intensively monitored bear and salmon occupation along the length of Connecticut Creek in 2015, when an estimated 101,216 sockeye salmon spawned over a 72-d period (based on video weir counts). However, because spawning salmon only survived an estimated average of 7.1 d (standard deviation = 3.5 d) after entering the stream, estimated maximum in-stream abundance was ~17,800 salmon in

late August (Figure 3.4a). Fish detection data from time-lapse cameras peaked first in the upper reaches and later in the middle and lower reaches (Figure 3.4b). The mean July–February daily water temperatures ranged from 4.3°C at the headwaters to 5.3°C near the stream mouth (Figure 3.4e). These temperatures were strongly correlated ( $r = 0.96$ ) with the median dates salmon were detected at different sites ( $n = 5$ ) along the stream (Figure 3.4b).

### ***Bear Fishing Pattern in Connecticut Creek***

Nine time-lapse cameras distributed between the headwaters and mouth of Connecticut Creek recorded 6573 bear detections in 2015 (Figure 3.4c). Daily activity peaked at 246 detections at the beginning of the salmon run on 13 July. Cumulative distributions indicate that peak bear activity varied along the length of the stream, peaking earliest for cameras at the headwaters and latest at the stream mouth (Figure 3.4d). Thus, the spatial and temporal patterning of bear activity tracked that of salmon.

### ***Bear Fishing Pattern at Other Focal Streams***

We lacked salmon presence data for streams other than Connecticut Creek, so we could not directly characterize within-site phenological variation across additional streams. As an alternative, we used patterns of bear presence to test for spatial variation in salmon phenology in six additional streams monitored in 2015. The bear detection pattern suggested there was spatial variation in spawning phenology at one site (Pinnell Creek) in addition to Connecticut Creek (Figure 3.5). Within-stream spatial variation in spawning did not seem to be present in the other five streams.

All analyses were performed using the open access statistical program R version 3.5.0 (R Development Core Team 2018).

## DISCUSSION

Recent research, including work in this consumer–resource system (Deacy et al. 2016a), has emphasized that among-population variation in the spawning phenology of salmon across the landscape prolongs landscape-level foraging opportunities for mobile consumers. We expanded on this work by exploring how within population phenological variation contributes to the spatial and temporal patterning of resource availability and consumer foraging. Across our focal landscape, salmon spawning duration varied roughly threefold among spawning sites (Figure 3.2a) and was strongly predicted by within site variation in spawning phenology (i.e., SD of arrival at spawning sites;  $R^2 = 0.81$ ). Bears seemed to be sensitive to this pattern; as within site variation in spawning phenology increased, so did the duration of bear foraging at sites (Figure 3.2d). The range of spawning durations observed (Figure 3.2a) would translate into a ~500 kg difference in per capita salmon consumption by brown bears constrained to consume salmon at a single site, based on recent empirical data relating seasonal foraging duration to salmon intake (Deacy et al. 2018). Thus, within-site variation is an important aspect of phenological diversity in salmon portfolios and interacts with among-site variation to influence the foraging ecology of bears and the fate of marine-derived nutrient subsidies to inland food webs.

Where runs were especially protracted, within site variation in spawn timing appears to be expressed spatially and was strongly correlated with thermal variation. At the most protracted spawning site, Connecticut Creek, spawning occurred first in colder upstream reaches and then shifted to warmer downstream reaches over a ~7-week period ( $r = 0.96$ , Figure 3.4b). However, many sites in our focal watersheds did not exhibit longitudinal variation in spawning phenology (as indicated by patterns of bear foraging), offering salmon

runs that were equally ephemeral at the reach- and stream-level scale (Figure 3.5). It is notable that the two longest sites (Connecticut Creek and Pinnell Creek) most clearly exhibited within-stream resource waves, most likely because longer streams have greater capacity for upstream–downstream patterns of warming (Caissie 2006). More work is needed to understand how fine-scale thermal heterogeneity influences intra-population variation in salmon spawn timing. Specifically, how do complex thermal mosaics on floodplains (Stanford et al. 2005, Tonolla et al. 2010) generate phenological diversity and to what extent does reproductive asynchrony increase predation risk (by preventing swamping of consumers) and potentially attenuate local adaptation to fine-scale thermal heterogeneity (Ims 1990, Takahashi and Sato 2017)?

While research has emphasized the magnitudes of among-stream thermal variation that drive inter-population variation in spawning phenology (Hodgson and Quinn 2002, Ruff et al. 2011, Lisi et al. 2013), these ranges in temperatures can also be expressed within single rivers (Webb and McLay 1996) and streams (Baldock et al. 2016, Uno 2016). This fine-scale variation can allow poikilotherm consumers to increase their consumption of salmon resources via behavioral thermoregulation (Armstrong et al. 2013) and can extend the duration of aquatic subsidies to terrestrial predators such as spiders (Uno 2016). Our results suggest that in some streams, such as Connecticut Creek, this fine scale thermal heterogeneity can increase consumption of salmon resources by generating within-stream resource waves that alleviate time constraints. Thus, fine-scale thermal heterogeneity can reduce the foraging limitations associated with ephemeral resources both by increasing maximum rates of energy intake and by prolonging resource availability.

While we demonstrate the role of within stream phenological variation in shaping the duration of salmon availability, there are additional mechanisms that allow bears and other mobile consumers to prolong site-level salmon foraging opportunities. Bears can potentially exploit migrating salmon in route to other spawning sites (e.g., streams draining lakes may be both spawning sites and migration corridors for salmon, Ruff et al. 2011), scavenge the carcasses of senescent salmon that persist after a run has subsided (Quinn and Buck 2000), and capitalize on multiple salmon species that spawn at different times at the same site (Levi et al. 2015). In the focal streams of this study, bears could scavenge senescent salmon, but did not have access to migrants or other species of salmon.

However, there are nearby sites where bears can intercept migrants and prey on multiple species of salmon (Deacy et al. 2016a). More research is needed to understand how these multiple factors contribute to the salmon foraging opportunities of bears.

The ecological effects of site-level spawning duration likely depend on the mobility of consumers. For more sedentary species that do not move among streams, an increase in duration likely provides a proportional increase in salmon consumption. For example, juvenile salmonids may rely heavily on salmon eggs for summer growth and do not appear to move among streams (Armstrong et al. 2013), so energy flows from spawning salmon to egg-consuming juveniles are likely highly sensitive to run duration. Mobile animals that track resource waves can sidestep this temporal constraint by fishing at several spawning sites with asynchronous runs; however, they likely face smaller penalties for sub-optimally moving among sites (e.g., arriving after peak spawning) when average duration is long and resource pulses overlap. For example, if a bear arrived at Connecticut Creek (our most protracted site) a month after the start of the salmon run, they would have access to salmon for another 40+

d. In contrast, at an ephemeral site such as Moraine Creek, a bear arriving 40 d after the onset of spawning would encounter no live salmon and few carcasses. Thus, site-level duration could mediate how sensitive trophic interactions are to the mobility and perceptual extent of consumers (*sensu* Lima and Zollner 1996). While recent theoretical models have explored how consumer behavior mediates the benefits of resource waves, such work has yet to explore multiple scales of phenological variation and has generally ignored within-site variation (Fryxell et al. 2005, Armstrong et al. 2016).

Tracking resource waves allows consumers to access resources for longer durations and has been linked to higher consumption (Deacy et al. 2018), growth (Ruff et al. 2011), and body mass (Mysterud et al. 2001, Pettorelli et al. 2005). However, there are likely trade-offs associated with phenological tracking, because movement costs energy (Shepard et al. 2013) and may increase predation risk (Middleton et al. 2013). For these reasons, locations that provide resources for long durations may be especially important for animals that are sensitive to movement costs (e.g., female bears with cubs; Ben-David et al. 2004). As human development pressure increases, duration of salmon spawning (rather than salmon abundance) could be a useful criterion for conservation prioritization. An abundant salmon run that is brief may be less valuable to consumers than the same number of salmon spread over a longer period, but more empirical studies are needed to quantify such benefits. It is also possible that spreading salmon across time could exacerbate agonistic interactions by reducing the daily abundance of salmon during a run, potentially increasing the predator-to-prey ratio (Abrams and Ginzburg 2000). More research is needed to untangle how salmon abundance, salmon run duration (Davis 2015), and interference competition interact to shape the foraging opportunities of bears and other consumers.

Prior work (Deacy et al. 2016a) combined with our results (Figure 3.4) suggests that large-scale patterns of salmon phenological variation are repeated at smaller scales in some watersheds. Bears appear to be sensitive to variation at two scales, tracking salmon waves both across landscapes and within individual streams. Other common resource waves are likely to have multiple scales of variation as well. Moose seem to track high-frequency changes in vegetation phenology with short-distance movements while simultaneously tracking landscape-scale phenological variation with infrequent long-distance movements (Van Moorter et al. 2013). Multi-scale phenological variation may also be important for migratory animals like mule deer and greater white-fronted geese that use stopover sites during long-distance migrations (Dingle and Drake 2007). These herbivores track green waves by timing their migrations with coarse-scale gradients in plant phenology (Sawyer and Kauffman 2011), but rather than moving slowly with the resource wave, they break up periods of rapid movement with periods of foraging at stopover sites. Although landscape- or continent-scale phenological variation influences the migration as a whole, it seems likely that local phenological variation influences the duration of stopovers. For example, mule deer move along broad-scale gradients in spring green-up (Aikens et al. 2017), but many other factors such as wind-drifted snow, aspect, and soil characteristics produce fine-scale heterogeneity in vegetation phenology (Hwang et al. 2011) that should increase the duration of quality foraging at local scales. An important challenge in movement ecology is to understand how phenological variation at multiple scales interacts to support wide-ranging consumers.



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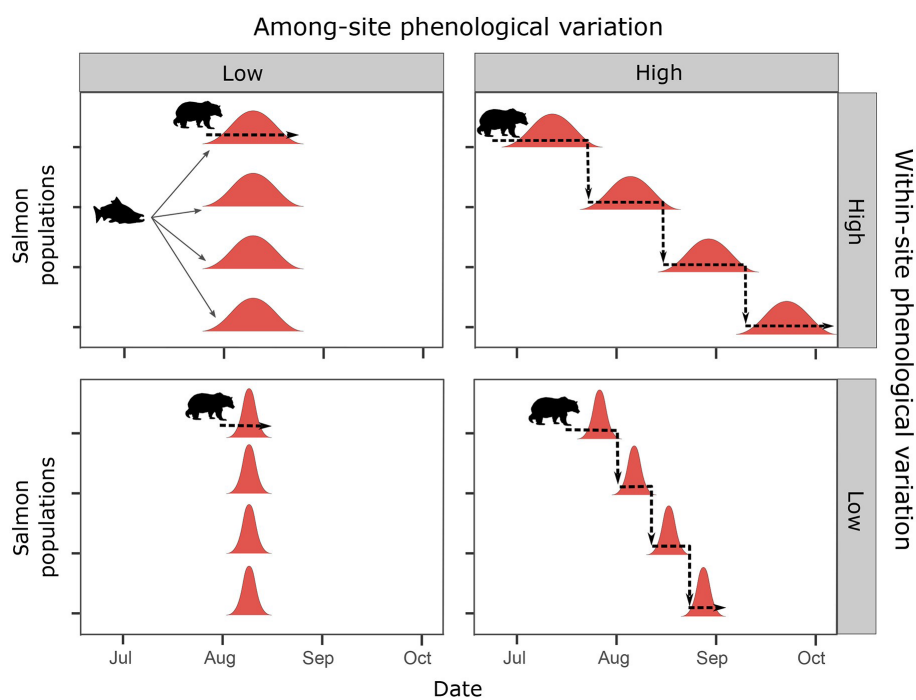
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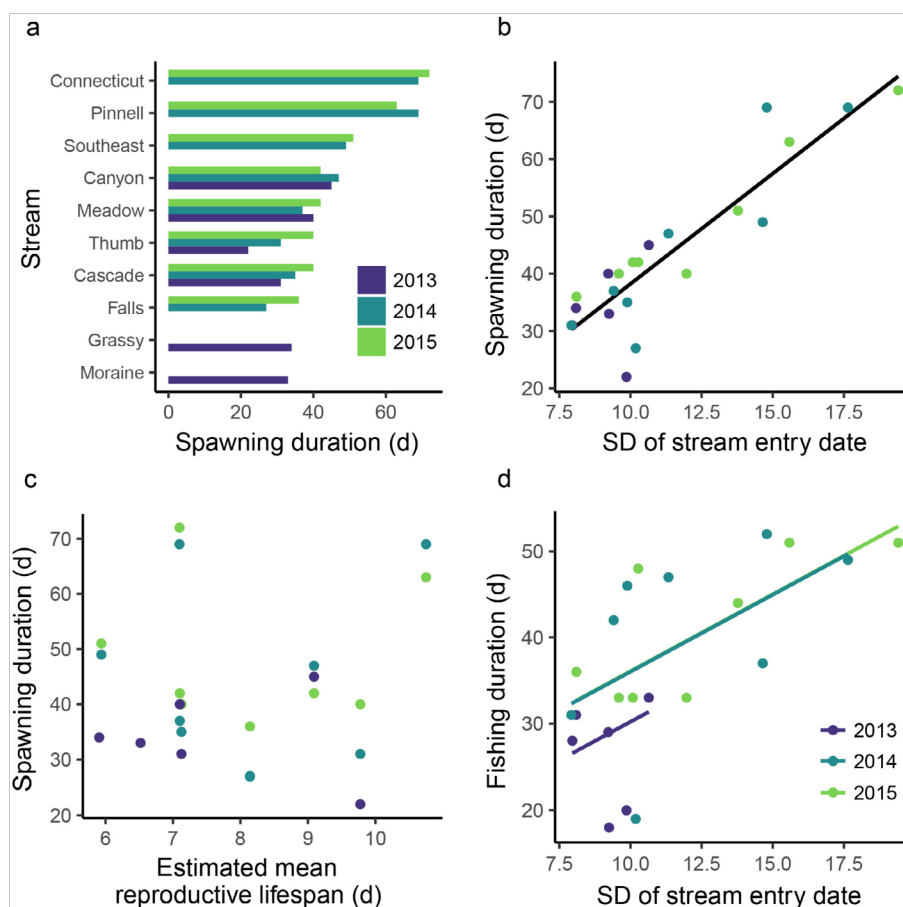
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## FIGURES

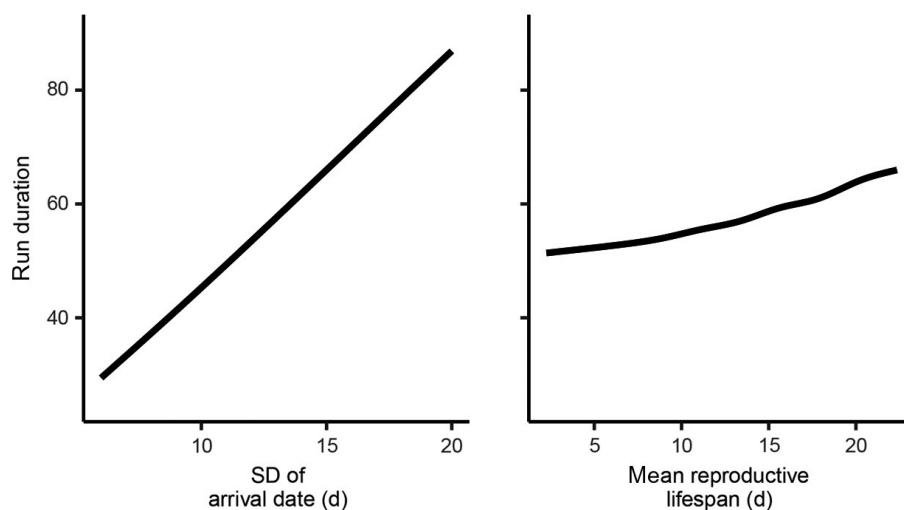
**Figure 3.1:** Schematic hypothesizing how different scales of variation in salmon spawning phenology affects the foraging opportunities and behavior of bears. The red distributions represent the abundance of spawning salmon in different populations, and the dotted lines show how an optimally foraging bear would move among the salmon populations. The panels show four combinations of two scales of phenological diversity, within and among spawning populations (or individual streams). Within-site phenological variation influences how long salmon spawn in an individual stream. Among-site phenological variation influences how long salmon are available at the landscape scale. Together, the two scales determine how long an optimally foraging bear can eat salmon and how frequently it must move.



**Figure 3.2:** (a) Sockeye salmon spawning duration in tributary streams, colored by year. Spawning duration was defined as the number of days where salmon abundance in streams exceeded 10% of the stream's maximum salmon abundance; (b) spawning duration as a function of standard deviation (SD) of sockeye salmon stream entry date ( $P < 0.0001$ ,  $R^2 = 0.81$ ). The black line shows a least-squares linear regression (there was no among year variation in intercepts) with equation  $y = 3.8490.263$ ; (c) spawning duration as a function of mean reproductive lifespan (number of days average sockeye salmon survives after entering a stream to spawn;  $P = 0.62$ ); (d) duration of bear occupancy of salmon spawning streams as a function of standard deviation (SD) in spawning site entry by salmon. Lines show linear regressions with random intercepts for year (likelihood ratio test,  $v_2(1) = 9.45$ ,  $P = 0.002$ ).

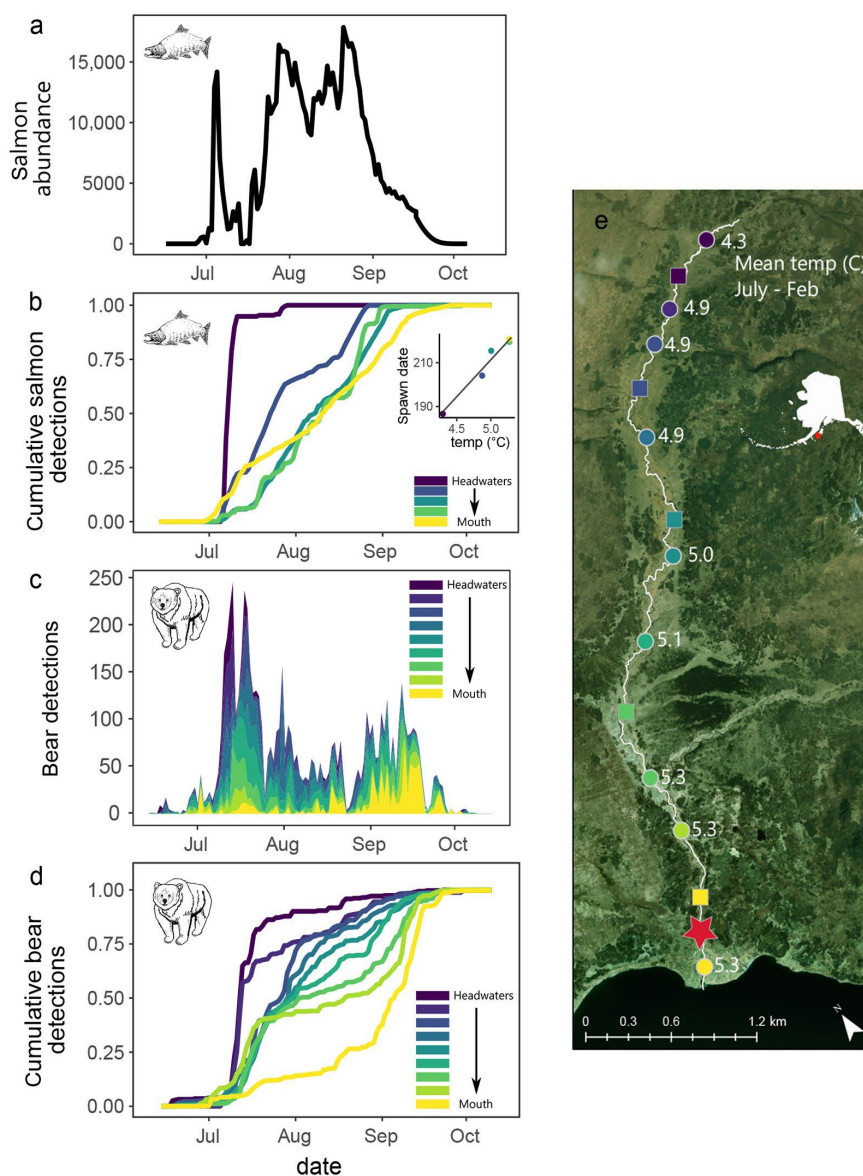


**Figure 3.3:** Results from simulations of how sockeye salmon run duration varies with two variables, arrival asynchrony (standard deviation (SD) of arrival date) and mean reproductive lifespan (the number of days the average salmon survives on the spawning grounds). In each simulation, the other variable was kept at its mean value. The range of SD of arrival dates is that observed in the study area, while the range of mean reproductive lifespan is that observed in a study area with similar characteristics in the Wood River basin, Alaska (Carlson et al. 2007). To help ensure the range in reproductive lifespan included plausible values for our study system, we increased the range from Carlson et al. (2007) by 50%. Run duration was defined as the number of days where salmon abundance exceeded 10% of peak salmon abundance.

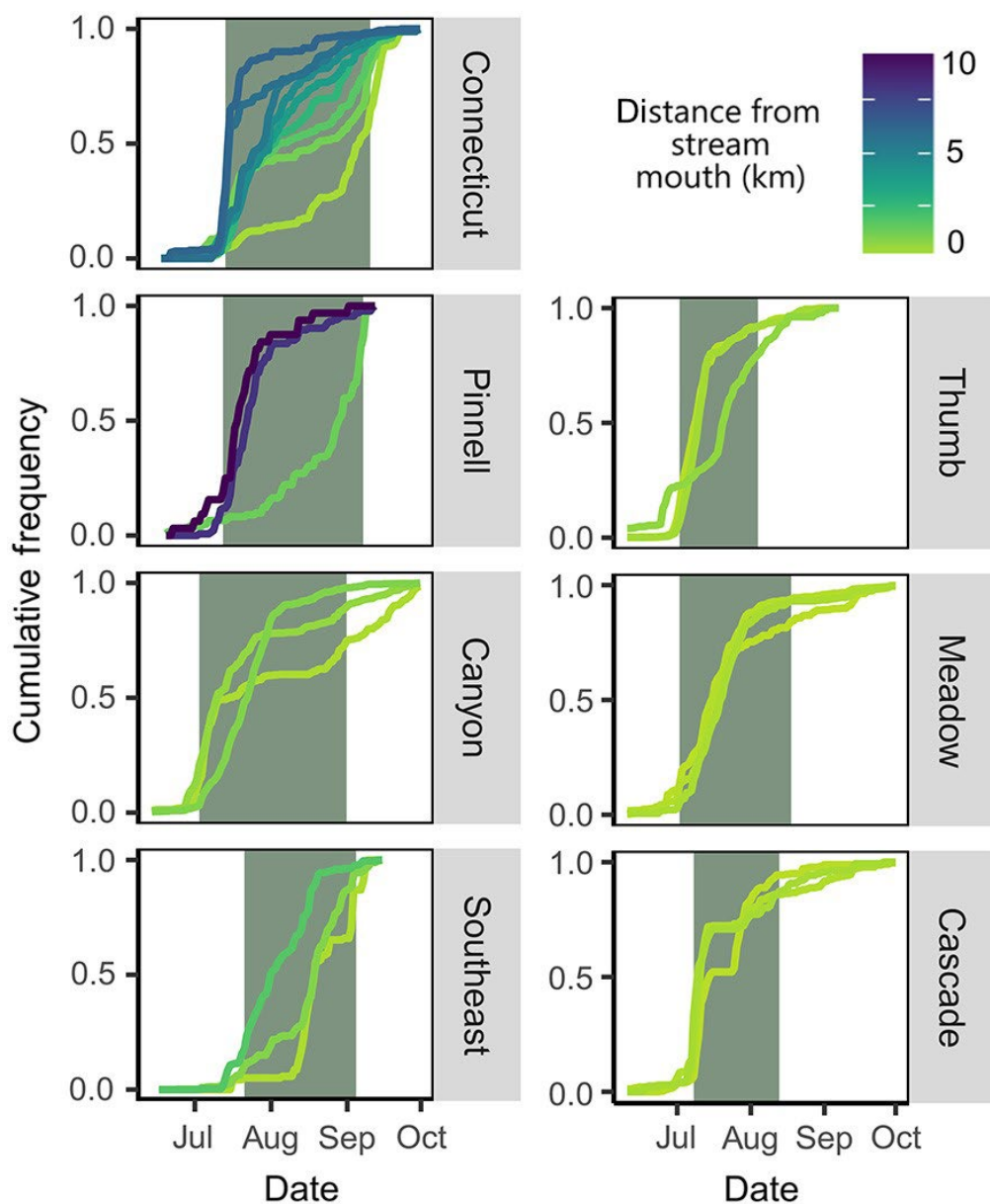




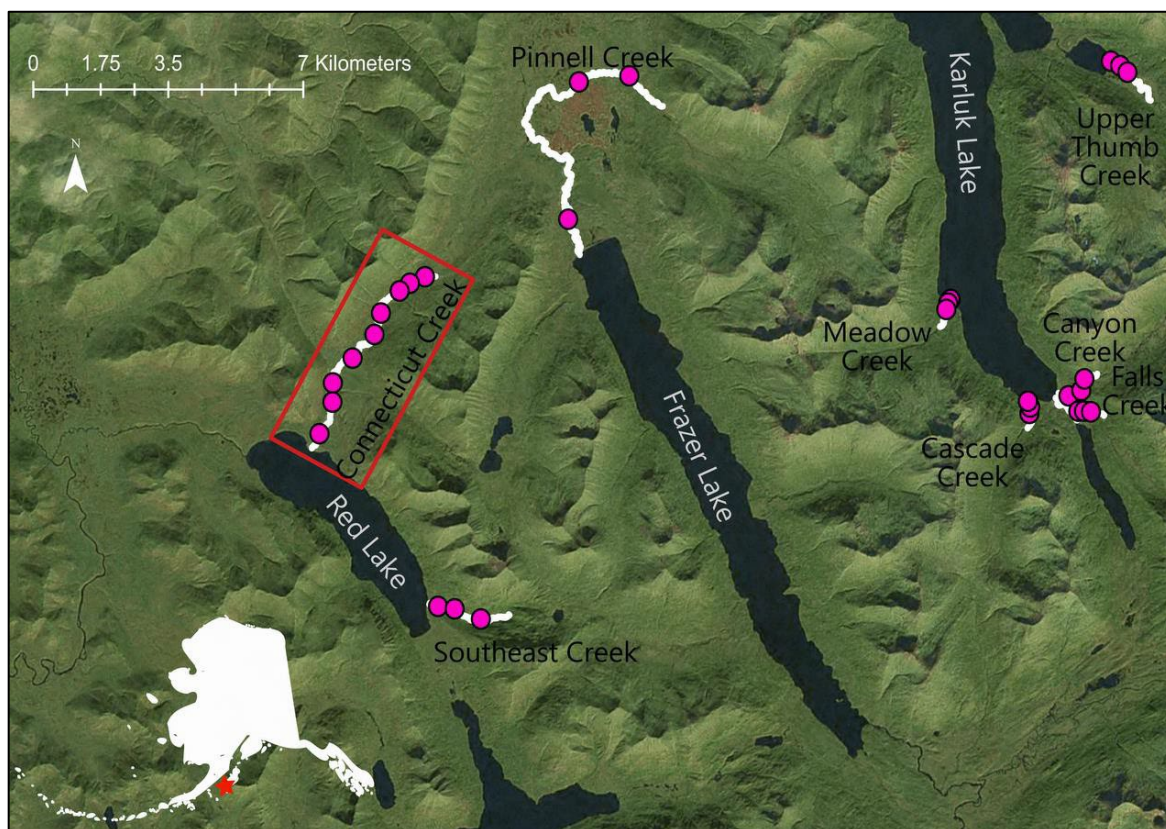
**Figure 3.4:** Brown bear response to spatial variation in sockeye salmon spawning phenology in Connecticut Creek, Kodiak Island, Alaska in 2015. (a) Salmon abundance during the spawning season. (b) Cumulative salmon detections from time-lapse cameras positioned along the watershed, colored by position in the watershed. Inset plot shows the median date of salmon detections (p50 of cumulative salmon detections) as a function of mean July–February temperatures ( $y = 33.78 + 42.45x$ ,  $P = 0.008$ ,  $n = 5$ ). (c) Stacked area plot of bear detections from nine time-lapse cameras spread along the stream. The color indicates where in the watershed bears were detected. (d) Cumulative distributions of bear detections through time, colored by watershed position. (e) Map of Connecticut Creek with markers for bear cameras (circles) and salmon cameras (squares). The mean July–February (approximate period of sockeye salmon incubation) temperatures are listed for each bear camera. Colors correspond to the colors in panels (b–d). The red star indicates the location of the salmon counting system used to produce the data in panel (a).



**Figure 3.5:** Cumulative distributions of brown bear detections at seven headwater streams in southwest Kodiak, Alaska, in 2015. Three time-lapse cameras were distributed along the stream reaches used by spawning sockeye salmon (except for Connecticut Creek which had nine cameras). The color of lines indicates the upstream distance of the camera relative to the stream mouth (see Figure S1 for map). The gray boxes show the duration of bear use at each stream, defined as the period between the 0.1 and the 0.9 of the cumulative distribution of bear detections (pooled across all cameras at a site).



**Figure 3.6:** Map of study area with bear camera locations (pink) and study streams (white). Red box shows the extent of map in Fig 4e in main article.



## Tables

**Table 3.1:** Morphology of study streams.

| <i>Stream</i> | <i>Spawning Length (km)</i> | <i>Mean Depth (cm)</i> | <i>Mean Width (m)</i> | <i>Watershed Area (km<sup>2</sup>)</i> |
|---------------|-----------------------------|------------------------|-----------------------|--|
| Pinnell       | 11.2                        | 25.9                   | 9.1                   | 101,121                                |
| Connecticut   | 6.7                         | 13.1                   | 5.6                   | 37,235                                 |
| Upper Thumb   | 3.0                         | 22.5                   | 10.5                  | 31,538                                 |
| Southeast     | 2.7                         | 9.1                    | 4.4                   | 11,635                                 |
| Falls         | 1.7                         | 16.8                   | 5.7                   | 9,845                                  |
| Canyon        | 1.4                         | 20.1                   | 9.0                   | 12,978                                 |
| Meadow        | 0.8                         | 13.2                   | 4.5                   | 3,668                                  |
| Cascade       | 0.8                         | 13.2                   | 4.7                   | 3,843                                  |

## CHAPTER 4

### KODIAK BROWN BEAR RESOURCE SELECTION FOLLOWING POST DEN EMERGENCE 2008–2015

#### *ABSTRACT*

Movement across the landscape by bears involves trade-offs among the needs of individuals. For example, bears need to balance risk avoidance, foraging needs, and travel. Resource selection likely varies among seasons and behavioral states. We evaluated the influence of behavioral state – resting, foraging, and traveling – on resource selection during the post-den emergence season – May 15 through June 30 for Kodiak brown bear (*Ursus arctos*). To accomplish this, we modeled resource selection of 54 radio-collared female brown bears over 86 unique bear-years from 2008 through 2015. We identified behavioral states by characterizing movement patterns according to speed and tortuosity and explored explanatory variables including landcover, topographic features, and NDVI for analyses to develop models at a study area scale. Our models allowed us to predict the relative probability of selection for different behavioral states. Selection models for the different behavioral states varied. Some covariates played similar roles across most models. Elderberry-salmonberry stands had a strong negative influence on selection; topographic position index had a moderate to strongly positive effect; NDVI had a moderately positive effect and stream length had a small positive influence across all behaviors. Edges among landcovers classes played different roles in selection when bears were resting, foraging, and traveling, but was not significant in models when all three behavioral states were combined. Dense alder and tree cover had a strong positive effect for resting behavior. The topographic

ruggedness index had a strong positive effect in models for resting, foraging, and when all three behavioral states were aggregated, but had no significant effect in the traveling behavior model. Our results emphasize the value of characterizing selection patterns according to behavioral state.

## **INTRODUCTION**

The study of animal movement and resource selection across the landscape plays a critical role in understanding ecological processes, wildlife management, and conservation efforts. The study of spatial ecology has received a great deal of attention over the recent past (Nathan 2008; Joo et al. 2020). Studies have included clarifications on concepts and terminology (Krausman 1999; Lele et al. 2013; Fieberg et al. 2021); general habitat selection and approaches (Aarts et al. 2008; Thurfjell et al. 2014; Edelhoff et al. 2016); identification of travel corridors (Abrahms et al. 2016; Zeller et al. 2017; Bastille-Roseu et al. 2021; Alavi et al. 2022); effects of anthropogenic factors (Tucker et al. 2018, Naidoo and Burton 2020); modeling statistical approaches (Hooten et al. 2014; Agar et al. 2016; Fieberg et al. 2020); and applications to conservation efforts (Fraser et al. 2018; Gerber and Northrup 2020).

Technical advances in wildlife telemetry have greatly improved our ability to collect large amounts of location data and monitor wildlife movements across the landscape (Thomas and Taylor 2006; Hebblewhite 2010; Seidel et al. 2018). These developments have helped us explore resource selection patterns among numerous wildlife species. Resource selection can be assessed through measures of use, nonuse, and availability (Manly et al. 2002). Used points are known, but unused points cannot be definitively identified. Partly as a result of this, use-availability study designs are often the most appropriate approach (Johnson et al. 2006). Furthermore, use-availability designs allow us to make inferences about

animals' choices (Jones 2001). Defining availability and defining temporal and spatial scale is a critical decision in study design. Four designs or orders are commonly used in habitat selection studies (Johnson 1980; Thomas and Taylor 2006).

The spatiotemporal arrangement of resources across the landscape and an animal's needs and aims influences movement and resource selection. Investigations into animal movement and resource selection are presented with challenges. These include identifying pertinent environmental covariates (Farhadinia et al. 2020), scale (Boyce 2006; Bastille-Rousseau et al. 2015), defining availability (Johnson et al. 2006; Thomas and Taylor 2006; Beyer et al. 2010; Northrup et al 2013), modeling and statistical procedures (Fieberg et al. 2010; Michelot et al. 2019; Fieberg et al. 2020 ), seasonal characteristics (Blake and Gese 2016; Buderman et al. 2021), and behavioral states (Roever et al. 2014; Gurarie et al. 2016; Gese et al. 2018 ).

Animals move deliberately across the landscape depending on their current needs, aims, and the distribution of resources. Intuitively, we'd expect resource selection to vary not only across seasons, but also according to behavioral states. Habitat needs and therefore resource use patterns often vary a great deal among behavioral states. Resource selection studies commonly compare locations used by wildlife with locations assumed to be available, but most studies have not discriminated among behavioral states, with a few notable exceptions (Wilson et al. 2012; Zeller et al. 2014; Roever et al. 2014; Gurarie et al. 2016; Ellington et al. 2020; Patin et al. 2020; Hance et al. 2021), which likely drive different patterns of resource selection. Melding behavioral states into one generic state can mask selection patterns (Schooley 1994).

Behavior specific analyses of habitat selection patterns of Kodiak brown bear can contribute to a better understanding of their spatio-temporal resource needs and the environmental features affecting these patterns and can contribute to developing effective conservation and management strategies.

Although there have been a number of valuable Kodiak brown bear studies, none have investigated selection within a seasonal-behavioral state framework. Atwell et al. (1980) characterized plant communities and brown bear use of alpine areas above Uganik Lake from 1973-1975. They documented regular use of these areas beginning around the first week of July, peaking during the second and third weeks of July. They foraged almost exclusively on large-awned sedge (*Carex machrochaeta*). Indeed, 97% of their foraging time was spent eating.

Barnes (1990) documented bear movement across the landscape to exploit salmon runs in southwest Kodiak. Van Daele et al. (1990) detailed bear denning patterns across Kodiak Island. They found that denning chronology and site selection varied across the island. Female bears in southwest Kodiak entered dens from two weeks to nearly a month later than bears in the Terror Lake region to the north. Den emergence was similar across the island with sows with cubs of the year emerging dens later than all other classes of bears. Denning periods ranged from 135 days for males to 205 days for sows with cubs of the year. In southwest Kodiak the mean den emergence date for sows without cubs was 28 April (ranged from 22 March-22 May); sows with older cubs 27 April (ranged from 11 March-8 June); and sows with cubs of the year 31 May (ranged from 7 May-3 July). Deacy et al. (2016) quantified bear travel behavior allowing them to more fully exploit the temporal diversity of sockeye salmon (*Oncorhynchus nerka*) runs across southwest Kodiak Island.



Sorum (2013) successfully carried out an innovative investigation of seasonal diets of Kodiak brown bears (*Ursus arctos middendorffi*) by using a combination of accelerometer activity data and patterns of GPS locations to identify recent bedding sites (resting behavior) where they collected scat samples for seasonal diet analyses and examined factors that influenced selection of bedding sites.

Berns et al. (1980) carried out an investigation into bear movement and habitat use based on VHF radio-telemetry data collected for 29 animals at Karluk Lake. Using 487 relocations they were able to draw a general picture of movement, spatial use, home ranges, and denning. They emphasized that more research and analyses are needed, especially during the period after den emergence. Yet, over four decades later, there have been no studies focusing on post-den emergence resource selection by Kodiak brown bear nor of behavior-specific resource selection. Ignoring behavioral states in our resource selection analyses can adversely affect our efforts to better understand habitat selection, species-habitat relationships, and the inferences we draw. With this paper we explored habitat selection by collared Kodiak brown bear sows during the post-den emergence period (May 15 – June 30) corresponding to three behavioral states: resting, foraging, and traveling. Our objectives were to 1) identify behavioral states for the post-den emergence season, 2) identify explanatory environmental variables associated with these behaviors, and 3) develop resource selection models for collared female brown bears at a study area scale for each of these behavioral states. We used a segmentation-clustering approach to identify behavioral states. We explored landscape variables that were suspected of possibly influencing habitat selection within each of the behavioral states and tested various selection models for each of these behavioral states. We expected habitat selection to be influenced by landcover class, edge,



stream length, topography, and NDVI (Landsat Normalized Difference Index) (Tables 4.1 & 4.2).

## **METHODS**

We developed design II (Manly et al. 2002) female brown bear resource selection models to evaluate environmental covariates that explained resource selection within the study area for three behaviors (resting, foraging, and traveling) during the period following den emergence (May 15 - June 30) from 2008-2015 on Kodiak Island. Bears were fitted with GPS transmitter collars (Telonics Model #TWG-3790) programmed to obtain hourly locations from 15 May to 15 November. We subset data to locations between 15 May and 30 June each year for analyses.

### ***Study Area***

The study area (Figure 4.1) encompasses the southwestern region of Kodiak National Wildlife Refuge that includes three primary salmon stream-lake systems (Karluk, Frazer, and Red), dozens of spawning tributaries and rivers, and a dense population of brown bears (~250 independent bears/1000 km<sup>2</sup>; Barnes et al. 1988). The region has a sub-arctic maritime climate characterized by cool temperatures (mean annual temperature of 2.08°C (-0.86° to 12.86°C monthly mean range), overcast skies, and heavy precipitation (198 cm rainfall and 175 cm snowfall) (Pyle and Hernandez, 2017). The topography of southwestern Kodiak ranges from sea level to 3,196 feet and is composed of a series of long fjords, a mixture of steep mountains, broad and short steep river valleys, lakes, gently rolling terrain, and wetlands. A mixture of deciduous tree species grow along rivers and streams. Lower elevation mountain slopes are covered in alder (*Alnus crispa*), salmonberry (*Rubus*

*spectabilis*), elderberry (*Sambucua racemosa*), ericaceous heathlands, and forb-graminoid meadows. Alpine and subalpine vegetation and barren areas are common at elevations above 760 m. Large areas of lowland heath and shrub-graminoid wetlands are common in the subdued rolling lowlands (Fleming and Spencer 2004). Human activity within the study area is limited and dominated by recreation, primarily hunting, sport fishing, and bear-viewing.

Each lake-stream system included in our study is somewhat unique. Karluk Lake is long (20 km) and relatively narrow (ranging from 1.4 km to 3.1 km wide) and has 11 tributaries, most of which are short and shallow and have spawning salmon runs during July and August. The exceptions are O'Malley and Thumb Creeks, which have relatively larger flows and drain larger valleys. Thumb Creek has sockeye salmon runs from July through August. Sockeye salmon transit through O'Malley Creek on their way to spawning grounds in Canyon and Falls Creeks during July and August. During September and October sockeye salmon spawn in O'Malley Creek. Karluk Lake is drained by the Karluk River, which is approximately 40 km long and flows into the ocean on the western side of the island near Karluk Village. Spawning sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) are available to bears in the upper 4.3 km of Karluk River during September and early October (Leacock et al. 2014). Sockeye salmon spawn on suitable shoals along the shore of Karluk Lake largely from September through November, but also to a lesser degree during July-August.

Frazer Lake is 14 km long and approximately 1.3 km wide, and has one primary tributary, Pinnell Creek. Dog Salmon Creek drains Frazer Lake and runs south approximately 14 km emptying into Olga Bay. The Frazer drainage is unique among the two other lake-river systems due to the fact that it supports an introduced sockeye salmon

population. Brood stock sockeye salmon were introduced into Frazer Lake from the Red Lake and Karluk Lake drainages during 1951-1971 (Blackett, 1979). Prior to 1962, a waterfall approximately one km below the lake outlet presented a barrier to salmon migration creating a terminal fishery. At that time a fish ladder was constructed at the waterfalls (Frazer Fish Pass), allowing spawning salmon to pass the waterfall and establish a self-sustaining population.

The third drainage consists of the Ayakulik River and the smallest of the three lakes, Red Lake. Red Lake is 6.4 km by 1.3 km and has two significant tributaries with sockeye salmon runs, Connecticut Creek and Southeast Creek. Red Lake is drained by Red Lake River (6.3 km long) flowing into the Ayakulik River which runs for 23 km to the ocean on the west side of the island. Salmon spawn in Southeast and Connecticut Creeks in July and August. Salmon transit through Red Lake River to Red Lake and Connecticut and Southeast Creeks during July and August and spawn in Red Lake River itself during September.

The Alaska Department of Fish and Game (ADF&G) monitors salmon escapement into each of these systems with fish weirs on the Karluk River, Ayakulik River, and Dog Salmon Creek and the Frazer Fish Pass. During the period 2006-2018 sockeye salmon returns to Karluk Lake averaged 481,000 (181,000 during the early run and 300,000 during the late run) ranging from 53,000 in 2009 to 295,000 in 2007; Frazer Lake averaged 139,000 and ranging from 90,000 in 2006 to 219,000 in 2015; and Ayakulik/Red Lake averaged 163,000 ranging from 59,000 in 2006 to 218,000 in 2015 (McKinley et al 2019).

Sturgeon River, in the far west of the study area, consists of two branches – the East Fork and the Main Stem. The Main Stem Sturgeon is approximately 35 kilometers long from the headwaters to the Sturgeon Lagoon. The East Fork Sturgeon is approximately 17 km

from its headwaters to the Sturgeon Lagoon. Both branches have chum salmon (*Oncorhynchus keta*) runs roughly between mid-June through mid-July (Price 2001). Runs on the Sturgeon River have been monitored only intermittently by fixed-wing surveys since 2000, but observations during annual aerial bear surveys from 2006 to 2018 suggest a substantial decrease in the size of salmon runs on both the Main Stem Sturgeon and East Fork Sturgeon.

### ***Capture and Monitoring***

We captured adult female brown bears in the SW region of Kodiak Island, Alaska. All bears were anesthetized via darting from helicopter using a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol<sup>®</sup>, Fort Dodge Laboratories, Fort Dodge, Iowa, USA) at a dose rate of 10-12 mg/kg (Taylor et al. 1989). Standard zoological measurements, weights, and age estimates were taken for each bear. Capture and handling procedures were approved by the Institutional Animal Care and Use Committees (ADFG ACUC 07-08, USFWS IACUC Permit 2012008, USFWS IACUC Permit 2012008 Renewal, and USFWS IACUC Permit 2015-001). We fitted each bear with a GPS radio collar (Telonics Model #TGW-3790) programmed to record a location every hour from 15 May through 15 November. Collars contained a UHF (ultrahigh frequency) radio transmitter and were downloaded using an airplane fitted with a UHF receiver. We screened GPS locations for accuracy, removing relocations with a positional dilution of precision (PDOP) greater than 10 (Lewis et al. 2007). We excluded bears from the analysis if their collars failed before acquiring at least 1500 relocations in a year. We selected bear locations restricted to the period 10 July through the end of August to coincide with the annual salmon run.

### *Environmental Covariates*

We evaluated resource selection of adult female brown bears using spatial covariates describing landcover and topographic features. Landcover covariates were derived from Kodiak Land Cover Classification 30 m raster data (Fleming and Spencer 2007), where we aggregated landcover into 13 classes (Table 4.3). We considered 10 of the 13 aggregated landcover classes including dense alder, elderberry/salmonberry, tree (alder/birch/cottonwood), tall willow, low willow, wetlands, meadows, lowland tundra, lowland bare, and freshwater. Each landcover class was created by binary reclassification such that values of 1 equaled the landcover class of interest and values of 0 equaled other landcover classes. We also created a covariate describing cover, which was an aggregate of dense alder, tall willow, and tree. For each landcover class, we calculated an edge diversity metric. The edge diversity metric was calculated for each landcover class as the absolute difference between the mean value of each raster cell and the 8 cells surrounding the center cell. Edge diversity ranged from 0 (all 8 surrounding raster cells were the same landcover class as the center cell) to 0.89 (all 8 surrounding cells represented a different landcover class than the center cell), and represented landscape diversity at the local scale. In addition we calculated a landscape uniqueness index which summed the number of unique landcover classes within the center cell and 8 surrounding cells (landscape uniqueness index values ranged from 1 to 9). We used package MODISsp in R (Busetto and Ranghetti 2016) to obtain 16 day composite Normalized Difference Vegetation Index (NDVI) rasters (250 m resolution; Didan 2015). NDVI estimates net plant primary production (Pettorelli et al. 2011).

To further refine layers representing water and to more accurately define salmon streams, we merged the water landcover class with stream layers that were developed

manually to create a comprehensive water covariate. Researchers walked study streams and recorded GPS locations every 10 meters to create a line feature that was smoothed across locations to characterize stream morphology. We used the shapefile generated from this effort and merged it with the water landcover layers creating the comprehensive water covariate/land cover class.

Covariates describing topography were derived from a 30 meter digital elevation model (DEM; US Geological Survey 2011). We calculated elevation, percent slope, roughness, Terrain Ruggedness Index (TRI), and Topographic Position Index (TPI) with the ‘raster’ package in R (Hijmans 2020). Roughness was calculated as the difference between maximum and minimum elevation of the raster cell and the 8 surrounding cells (Wilson et al. 2007). Ruggedness (TRI) is a measure of local terrain variation and was calculated as the mean of the absolute difference between the elevation at the location/center cell and each of the 8 surrounding cells (Wilson et al. 2007). Topographic position index (TPI) is a method to identify the relative position of a point along a topographic gradient, i.e., along a ridge, mid-slope, or valley. TPI compared the elevation of each cell to the mean elevation of the 8 surrounding cells (Guisan et al. 1999). Positive TPI values correspond to ridges or hilltops, negative TPI values are indicative of topographic depressions within the surrounding landscape such as valleys, gullies, and mountain passes, and values approaching 0 are indicative of flatter topography and mid-slopes (Weiss 2000; Knitter et al. 2019).

### ***Defining Bear Movement Behavior***

We modeled behavioral states of 51 radio-collared female Kodiak brown bears over 76 bear-years from 2008-2015 during the post-denning emergence season (May 15 – June 30) to investigate resource selection associated with each of these behavioral states.

Movement patterns can be characterized according to speed and tortuosity (Zeller et al. 2014; Edelhoff et al. 2016; Gurarie et al. 2016; Patin et al. 2020). Movement behavior for bears can be classified into three biologically meaningful states: resting, foraging, and travel or transit (Patin et al. 2020; Clontz et al. 2021). Resting behavior is characterized by little movement and low activity. Foraging behavior is indicated by high tortuosity and low speed. Transit or travel behavior is characterized by low tortuosity and higher speed (Patin et al. 2020). We used a segmentation clustering method with the *seglust2d* package in R (Patin et al. 2019) to identify different movement behaviors of female brown bears for use in our models. This approach followed a modified version of Lavielle's method (Lavielle 1999) to detect change points between behavioral states in a time series of GPS locations for each individual (Ducros et al. 2020, Patin et al. 2020). We used speed and relative turning angle between successive one hour re-locations to differentiate behavioral states. We considered 3 behavioral states, or clusters, in our models that we defined as resting, foraging, and travel/transit. The minimum number of locations for each segment,  $L_{min}$ , was set to 5 (Patin et al. 2019). As a validation of this clustering technique to identify behavioral states, we used the activity sensor data on board the radio-telemetry collars collected with each bear location. We used an analysis of variance to evaluate whether mean activity sensor values from the transmitters differed significantly from each behavioral state identified with the segmentation clustering method. Activity sensor values were log transformed to ensure that data fit a normal distribution.

### ***Resource Selection Analysis***

We estimated four resource selection functions (hereafter, RSF) for female brown bears with all locations (aggregated behaviors) and for each of the three behavioral states

(resting, foraging, and travel) separately using binomial generalized mixed models with package lme4 in R (Bates et al. 2015). We used an individual bear intercept term nested within year in the model to account for individual variation and possible variation in individuals across years, as well as to address the issue of pseudo-replication within individuals (Gillies et al. 2006). We manually digitized a polygon surrounding pooled locations of all bears and then buffered the all-bears polygon by the average movement distance between bear locations. We considered this the study area and we randomly generated 10 available locations per bear-use location to represent available habitat across the study area. We extracted covariate values at each used and available location. For RSF models we assessed environmental covariates within a 275-m circular region. This buffer represented half of the average distance traveled by female brown bears between relocations, and therefore buffered average values within 275 m are likely better representations of the environment at the scale of bear selection (Smith et al. 2020). For land cover covariates, we calculated the proportion of each landcover class within the circular buffer. For edge diversity and topography predictors, we calculated the mean values within the circular analysis buffer. We centered and scaled variables to ensure model convergence prior to modelling (Becker et al. 1988). The RSF took the following form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$$

where  $w(x)$  was proportional to the probability of female brown bear selection and  $\beta_1$  represented the coefficient describing selection strength for covariate  $x_1$ , and  $n$  represented the number of covariates in the model.



### ***Model Selection and Validation***

We used a variable subsetting approach (Arnold 2010) to develop nested candidate models and determine the most parsimonious set of covariates to describe selection by female brown bears during the post-den emergence season (May 15-June 30). We started by exploring all variable combinations within landcover, edge diversity, and topography variables separately in subset models (Tables 4.3-4.6). We did not allow variables in the same model when they were highly correlated ( $|r| > 0.75$ ) and set the maximum number of variables in any model at 4. We retained variables in the most predictive models from each subset and explored all combinations of remaining variables including the length of salmon stream covariate. We ensured that correlated variables were not included in the same model and set the maximum number of variables in any model at 8 to avoid potential model overfitting. Candidate models were fit with package MuMIn in R (Barton 2020). We used Akaike's Information Criterion (AIC) to assess support for all models (Burnham and Anderson 2002) and considered models within 2 AIC of the best model to be competitive. If AIC scores were nearly equivalent (i.e., within 2 AIC), we evaluated support of individual covariates by evaluating their 95% confidence intervals (Burnham and Anderson 2002, Arnold 2010). Once we arrived at a final model, we added the NDVI covariate to assess model improvement. NDVI estimates were available every 16 days, so we matched bear locations to the nearest date associated with the NDVI composite raster data.

We used 5-fold cross validations to evaluate the most-supported RSF models (Tables 4.7 and 4.8). We performed validations for both models that contained and did not contain the NDVI covariate. For models containing NDVI, we averaged NDVI composites collected nearest to 15-June each year to develop and average NDVI over the study period to be used

for spatial predictions in each validation. Data were randomly partitioned by individual bear-years. We estimated predictions based on 4 of the 5 groups (training data) and compared them to the withheld group, and repeated this until the 5 withheld groups were evaluated (Johnson et al. 2006). We binned predictions into 6 equal-area (quartile) intervals (Wiens et al. 2008). Validations were performed by running simple linear regression models on the number of observed locations from the test group compared to expected locations generated from each RSF bin (Johnson et al. 2006). We considered models to be good predictors when linear regression models had high coefficients of determination ( $r^2 > 0.9$ ) and 95% confidence intervals of slope estimates excluded zero and included 1 (Howlin et al. 2004). We mapped the most predictive RSF model across the study area by using coefficients from the top model and distributed predictions into 6 equal area bins corresponding to increasing relative probability of selection.

## RESULTS

We used data collected from 54 female brown bears with 86 unique bear-years spanning 2008-2015. We evaluated models for all behaviors combined (aggregated) and each of the three identified behaviors – resting/stationary, foraging, and travel. We estimated an overall RSF using 36,590 locations. We estimated stationary, foraging, and travel behavior RSFs with 8,605, 17,279, and 10,706 locations, respectively. For each analysis, inclusion of NDVI resulted in better model fit. Nonetheless, spatial predictions of RSFs for the aggregated behavioral states model and each behavioral state model were considered acceptable to good predictors of brown bear resource selection whether or not they included NDVI. Parameter estimates with 95% confidence intervals for covariates included in RSF models are summarized in Tables 4.9 and 4.10.

When all three behavioral states were included, the best model was comprised of the covariates tree cover, elderberry-salmonberry stands, lowland tundra, meadows, elevation, TPI, TRI, stream length and NDVI. Cover and TRI were strongly positively correlated with use. Elevation, stream length and NDVI were also positively correlated with use, but more weakly. Elderberry-salmonberry stands, meadows and TPI had strong negative effects on use (Table 4.11).

The inclusion of the covariates dense alder, elderberry-salmonberry stands, tree cover, lowland tundra edge, elevation, TPI, TRI, stream length, and NDVI provided the best model for stationary or resting behavior. Dense alder, tree cover, elevation, and TRI had a strong positive association with habitat use. Stream length and NDVI had weaker positive effects. Elderberry-salmonberry stands and lowland tundra edge had strong negative effects while TPI had a weaker negative influence.

The best foraging behavior model included the covariates cover, elderberry-salmonberry, meadows, lowland tundra edge, meadows edge, TPI, TRI, and stream length. The covariates cover, meadows edge, TRI, stream length, and NDVI. TRI, cover, meadows edge, NDVI, and stream length had a positive effect on use. Elderberry-salmonberry stands, meadows, lowland tundra edge and TPI had strong negative effects on use.

The best travel behavior model included the covariates cover, elder-berry-salmonberry stands, lowland tundra, tree edge, water edge, elevation, TPI, stream length, and NDVI. Cover and elevation had a strong positive influence on travel. Tree edge, water edge, NDVI, and stream length were positively associated with use. Elderberry-salmonberry has a strong negative effect on use while traveling. Lowland tundra and TPI had weaker negative effects on use.

## DISCUSSION

Resource availability, use, movement, resource selection patterns and the factors that influence these patterns may vary across seasons (Ciarniello et al 2007; Gese et al. 2018; Richter et al. 2020). Therefore, depending on the questions being asked, use and availability may be measured annually, within seasons or other biologically meaningful periods, and/or according to diel patterns (Moore et al. 2002). An animal's objectives, motives, and choices also likely vary both within and across seasons. This would be reflected in an animal's behavioral state. Yet, determining behavioral states has posed difficulties, especially since many species may be cryptic or range over such large areas that individuals cannot be observed consistently over time. Through radio-telemetry we are able to collect data on a regular basis providing systematic locations for monitored animals and possibilities for more detailed analyses.

Using direct observations in the Lamar Valley of Yellowstone National Park, Wilson et al. (2012) carried out a study comparing resource selection models of coyote (*Canis latrans*) during the gestation period partitioned by behavioral state (predatory, resting/laying, and traveling) versus all behaviors combined into one category. Their research found that resource selection differed among behaviors and differed markedly from resource selection when behaviors were clumped together. They emphasized that by partitioning behaviors the inferences about selection patterns are not only enhanced, but offer important insights and implications for management and conservation strategies.

Zeller et al. (2014) used mixed-effects conditional logistic regression models with a used-available design to examine point selection for pumas across a range of scales and two behavioral states (resource use and travel) to estimate landscape resistance. Two behavioral

states were identified – 1) resource uses that are typified by slow tortuous movement patterns that often produce clusters of points and could include a variety of behaviors for example, feeding, resting, and use of day beds and 2) travel which is distinguished by faster more direct movement patterns. They found that inferences regarding resources selection is influenced by both scale and behavioral state.

Ellington et al. (2020) carried out an innovative study of how resource selection by coyotes in Nova Scotia changes with behavioral state (encamped, foraging, and traveling), and time of day. They found a difference in time spent in encampment behavior between the snow-free season versus the snow season (longer periods of rest during the snow season). Foraging behavior was more frequent during the snow-free period. During the snow-free season coyotes selected for open cover during the day, but avoided these areas during crepuscular and nocturnal periods preferring open forest edges and diverse landscape. Whereas during the snow season coyotes preferred forested areas during the day and crepuscular periods avoiding open and closed forest areas and heterogeneous landscapes during the day. Overall travel behavior varied between the snow season and the snow-free period by time of day. They suggest that their study emphasizes that animals, at least partly, make decisions based on perceived costs and benefits in a more complex manner than has commonly been recognized and that ignoring behavioral state, season, and diel differences impedes our ability to not only better understand resource selection by the animals of our research, but also the effectiveness of our management and conservation efforts.

Clontz et al. (2021) used Hidden Markov Models (HMMs) to analyze movement patterns and identify associated behaviors (resting, foraging, and travelling) of wild pigs (*Sus scrofa*) in the Savannah River valley near the Georgia-South Carolina border to then develop

behavior-specific resource selection models according to season. Wild pigs selected for different landscape attributes depending on their behavioral state.

Hance et al. (2021) used GPS collar and accelerometer data and an HMM to successfully differentiate movement and resting behaviors to identify resting sites (a critical habitat component) for fishers (*Pekania pennant*) in Oregon and California. This allowed them not only to advance understanding of fisher ecology, but to also help design more valuable and practical management strategies.

There have been few brown bear studies investigating post-den emergence resource selection. Gardner et al. (2014) explored movement and the spatial ecology of maternal grizzly bears sows and the survival of first-year cubs in the eastern interior of Alaska. Mortality rates of cubs during their first year, between den emergence and den entrance in the autumn was 61%. Sixty-nine percent of cub deaths occurred between May 31-June 16. They found that sows with surviving cubs tended to travel less during morning hours (midnight to noon) than sows who lost their cubs. Between May 15-June 30 sows with first-year cubs had significantly smaller home ranges than sows with older cubs and lone sows. Sows with cubs travelled shorter daily distances than lone sows. After sows lost their litter they promptly had similar home range sizes and movement rates as lone sows. They were unable to determine whether cub mortality was due to infanticide or access to resources (forage) since they did not measure habitat use of sows and did not have movement data for male bears. They conclude that sows with first-year cubs were able to maximize cub survival by limiting activity between midnight and noon and by limiting movements between den-emergence and spring green-up.

Karelius et al. (2019) carried out a study of black bears in Florida to investigate habitat selection by incorporating behavioral states and movement patterns into their analyses. They identified three behavioral states resting, encamped (foraging), and traveling. They found that habitat selection varied with behavioral state. While encamped (foraging) and traveling, bears selected for forested and marsh wetlands, selected areas more distant from roads and to a lesser degree creeks, and avoided urban, rural, and agricultural areas. While resting bears selected for forested wetlands, urban, rural, and agricultural areas, but distance to roads and creeks had no effect. They emphasized that by investigating habitat selection relative to season and behavioral state that managers would be able to make more informed decisions regarding habitat protections and the preservation of connectivity across the landscape.

This work presents the first detailed analysis of post-den emergence resource selection for Kodiak brown bear based on behavioral states. We hypothesized that resource selection would vary among behavioral states and that relying on an aggregate of all behaviors could be misleading or incomplete and could produce less than ideal inferences. Indeed, models based on different behavioral states did differ, though some of the environmental drivers were shared across all behaviors.

It was anticipated that tree cover, elevation, and greater ruggedness would be strongly selected for during resting behavior. We reasoned that selection for these covariates would provide more protection or risk avoidance for female bears. Field observations indicate that day beds are often found within denser vegetation, with the exception of elderberry-salmonberry stands. Skuban et al. (2018) found that brown bears in Slovakia selected forests with dense horizontal cover for day beds. Mysterud (1983) documented that brown bears in Norway commonly excavated day beds in dense spruce stands. Dense tree stands are more

difficult to navigate through than more open landscapes and may provide auditory cues to risks from other bears moving through this vegetation type. Additionally, tree cover also provides benefits to thermoregulation (Pigeon et al. 2016). Indeed, there was strong selection for dense alder and tree stands.

Field observations also suggest that bears, especially female bears with cubs, often select bedding sites with good fields of view and topographically more difficult terrain to travel across. This often includes higher elevations and areas with knolls, outcroppings, and cliffs. Mollohan (1987) found that female black bears (*U. americanus*) in northern Arizona selected bedding sites on canyon walls, steep slopes, and denser forest stands. In a study in Slovakia sows with cubs of the year often selected for rugged terrain during spring and early summer (Skuban et al. 2018). Therefore, we expected higher elevations and more rugged topographic areas to be frequently selected for. When resting, bears did indeed select for higher elevations and more rugged terrain. We expected a positive relationship with TPI with bears selecting for ridges or similar topographic features, but the relationship was mildly negative.

There was moderately strong selection for NDVI. We did not anticipate this. A possible explanation for this could be that bears are selecting resting sites with foraging areas nearby (Sorum 2013; Skuban et al. 2018). Gardner et al. (2014) found a positive relationship between smaller spring home ranges and reduced travel with increased cub of the year survival. Selecting for safe resting sites near areas with higher NDVI values and thus foraging opportunities fits with this pattern.

Cover, meadow edge, terrain ruggedness, NDVI, and stream length were strongly correlated with foraging behavior. The cover and stream length land cover classes are largely



found at lower elevations and there is often an early spring flush of growth of some forb and grass species along streams and in the understory before trees leaf out. It is surprising there was strong selection against meadows, yet selection for meadow edge for foraging. We did not predict a positive relationship with meadow edge, but we did for the meadow land cover class. Model results were contrary to both of these expectations.

Results from our model of travel behavior were surprising in a few ways. Bears strongly selected for the cover class and only weakly selected for tree edge and stream length for travel. Bear trails are often observed along streams and where tree stands meet more open vegetation types. Perhaps these travel paths are not commonly used extensively for travel until later in the season. As expected water edge and elevation were selected for when traveling. Riverbanks and lakeshores provide easy travel routes. They are commonly open and void of obstructions. Dens, of course, tend to occur at higher elevations (Van Daele et al. 1990), these areas tend to retain snow well into early summer and thus generally provide easy travel routes.

Most years, salmonberry stands do not begin to bear ripe fruit until late July and elderberry not until mid to late August. Elderberry and salmonberry stands tend to be very dense and present relatively impenetrable obstructions. Lowland tundra is relatively barren of food resources and is characterized by widespread hummocks making travel more onerous than many other land cover types. Therefore, we would not expect bears to use these land cover classes to much of an extent during May and June. Indeed, our models indicated this.

Normalized Difference Vegetation Index (NDVI) is commonly used as a metric for forage quality (Pettorelli et al. 2005, 2011). A study of black bears (*Ursus americanus*) found that NDVI was a good predictor of spring foraging patterns (Bowerstock et al. 2021).

In our study NDVI had a positive influence on selection across all behavioral states. It was expected that NDVI would have the strongest effect during foraging behavior, but interestingly its effect was no stronger during foraging behavior than any other behaviors with the exception of travel behavior.

Our models revealed significant differences in habitat selection among behavioral states during the post-denning emergence season. This was especially true when compared to the model in which behaviors were aggregated to models in which behavioral states were modeled separately. When all behaviors were aggregated into one, the model often failed to identify factors that were strong predictors of selection patterns for specific behavioral states.

There are a few recommendations we would pose as worthy of future research to address a few of the limitations of our study. Our study focused on habitat selection by female bears. It would be valuable to include male bears in a future study to investigate possible behavioral and selection effects of interactions among females and males. Due to a small sample size of sows with cubs we did not investigate differences between sows with cubs and lone sows. It is likely that there are significant differences. Our edge and landscape diversity metrics may not adequately capture the influence of the landscape mosaic and its effect on selection patterns. We need to develop better metrics to more effectively capture the influence of landcover matrices, associations among different landcover classes, and shapes of these landcover patches. We believe that not only does diversity within a buffer around used locations influence selection, but also that the arrangement and specific associations among different landcover classes plays important roles. For example, are graminoid meadows more likely to be exploited if they are near or adjacent to dense alder or *Vaccinium* communities or another land cover type? Also, does the shape of a land cover

patch influence use? For example, is a meadow with a circular shape more likely or less likely to be used than a more irregularly shaped meadow? We did not investigate the role of time of day on selection and interactions with behavioral states. Additionally, it would be valuable to carry out and compare behavioral state habitat selection patterns across seasons. And finally, it would be informative to carry out a multi-scale investigation of resource selection for these behavioral states, in particular a fine-scale study employing step-selection functions could make a valuable contribution to a better understanding to the spatial ecology of the Kodiak brown bear.

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## TABLES

**Table 4.1:** Description and Justification of Factors Behavioral State Models for female brown bears post den emergence on Kodiak Island

| Categories of Factors     | Description   | Justification   |
|---------------------------|---|---|
| <b><u>Landcover</u></b>   |   |   |
| Cover                     | Aggregate of alder ( <i>Alnus crispa</i> ), tall willow, and tree   | May provide thermal and/or risk avoidance refuge  |
| Elderberry<br>Salmonberry | Dense stands of <i>Sambucus racemosa</i> and/or <i>Rubus spectabilis</i>  | Dense stands hinder movement.<br>Fruiting after June  |
| Lowland tundra            | Low elevation heath dominated by Ericaceous dwarf shrubs, mats of moss ( <i>Racomitrium lanuginosum</i> ), and fruiticose lichens often with many hummocks  | Largely void of forage in May-June and dense hummocks impede movement   |
| Meadows                   | Graminoid forb stands   | Lower elevation and south-facing may provide early season forage in May-June  |
| Dense alder               | Open alder stands (60-100% cover)   | May provide thermal and/or risk avoidance refuge  |
| Tree                      | Open alder, birch ( <i>Betula kenaica</i> ), cottonwood ( <i>Populus balsamifera</i> ), and occasional tall willow ( <i>Salix stichensis</i> , <i>S. alexensis</i> ) stands, with understory often with ferns, forbs, and grasses | Movement relatively unrestricted and may have early season forb and grass forage available.   |
| Edge                      | Edges between land cover types including water  | Edges between land cover types often offers easy travel routes and access to multiple resources associated with those land covers, such as forage and/or escape cover |
| Stream length             | Length of stream within 275 meter buffer  | Provides easy travel corridors, early season forage, and salmon   |

Table 4.1: cont'd

| Categories of Factors    | Description  | Justification  |
|--------------------------|--|--|
| <b><u>Topography</u></b> |  |  |
| Elevation                | Elevation above sea level  | Den sites at higher elevations, open land cover, higher elevations covered in snow in May-June |
| TPI                      | Topographic Position Index; relative position of a point along a topographic gradient, i.e., along a ridge (+ values), flatter areas and mid-slope areas (values approaching 0), or depressions within the local area (- values) | May influence travel, risk avoidance, and forage availability                                  |
| TRI                      | Terrain Ruggedness Index; a measure of local topographic variation   | TRI may influence access to sites for risk avoidance, forage availability, and movement        |
| <b><u>NDVI</u></b>       | NDVI estimates net plant primary production  | A measure of potential forage availability   |

**Table 4.2:** Working Predictions for Behavioral State Models for female brown bears post den emergence on Kodiak Island

| Categories of Factors     | Prediction                         |                                    |                                  |                                 |
|---------------------------|------------------------------------|------------------------------------|----------------------------------|---------------------------------|
|                           | <i>All Behavioral States</i>       | <i>Stationary Behavioral State</i> | <i>Foraging Behavioral State</i> | <i>Travel Behavioral State</i>  |
| <b><u>Landcover</u></b>   |                                    |                                    |                                  |                                 |
| Cover                     | Select                             | Select                             | Select                           | Avoid                           |
| Elderberry<br>Salmonberry | Avoid                              | Avoid                              | Avoid                            | Avoid                           |
| Lowland tundra            | Avoid                              | Avoid                              | Avoid                            | Avoid                           |
| Meadows                   | Select                             | Neither avoid<br>nor select for    | Select                           | Neither avoid<br>nor select for |
| Dense alder               | Neither avoid<br>nor select        | Select                             | Avoid                            | Avoid                           |
| Edge                      | Select                             | Neither avoid<br>nor select        | Neither avoid<br>nor select      | Select                          |
| Stream length             | Neither avoid<br>nor select        | Avoid                              | Select                           |                                 |
| <b><u>Topography</u></b>  |                                    |                                    |                                  |                                 |
| Elevation                 | Neither avoid<br>nor select        | Select higher<br>elevations        | Avoid higher<br>elevation        | Select higher<br>elevation      |
| TPI                       | Neither avoid<br>nor select        | Select for<br>depressions          | Select for<br>depressions        | Select for<br>depressions       |
| TRI                       | Select for<br>greater<br>variation | Select for<br>greater<br>variation | Select for greater<br>variation  | Select for less<br>rugged areas |
| <b><u>NDVI</u></b>        | Mildly select                      | Neither avoid<br>nor select        | Select                           | Neither avoid<br>nor select     |

**Table 4.3:** Reclassification of Kodiak Island Land Cover Classification by Fleming and Spencer 2007.

| <b>Original Landcover Class</b>     | <b>Analysis Landcover Class</b>      |
|-------------------------------------|--------------------------------------|
| Alpine Forb Meadow                  | Alpine tundra                        |
| Alpine Heath                        | Alpine tundra                        |
| Alpine Tundra                       | Alpine tundra                        |
| Prostrate Shrub Tundra              | Alpine tundra                        |
| Bedrock                             | Rock/snow                            |
| Snow and Permanent Ice              | Rock/snow                            |
| Talus                               | Rock/snow                            |
| Heath/Bedrock                       | Rock/snow                            |
| Clear fresh water                   | Fresh water                          |
| Shallow fresh water                 | Fresh water                          |
| Aquatic Emergents                   | Marine                               |
| Eelgrass                            | Marine                               |
| Marine water-Low Sediment           | Marine                               |
| Marine water-Shallow/Sediment       | Marine                               |
| Marine water-Shallow/Sediment       | Marine                               |
| Goose Tongue                        | Marine                               |
| Alder-Willow Mix                    | Dense Alder                          |
| Dense Alder                         | Dense Alder                          |
| Open Alder-Salmonberry-Elderberry   | Elderberry-Salmonberry               |
| Salmonberry/Forb Meadow             | Elderberry-Salmonberry               |
| Salmonberry-Devil's Club-Elderberry | Elderberry-Salmonberry               |
| Salmonberry-Elderberry              | Elderberry-Salmonberry               |
| Cottonwood-Birch & Alder            | Alder-birch-cottonwood-spruce (Tree) |
| Dense Birch                         | Alder-birch-cottonwood-spruce (Tree) |
| Dense Cottonwood                    | Alder-birch-cottonwood-spruce (Tree) |
| Open Alder-Forb Meadow              | Alder-birch-cottonwood-spruce (Tree) |
| Open Alder-trace Cottonwood-Birch   | Alder-birch-cottonwood-spruce (Tree) |
| Open Alder-trace Sitka Spruce       | Alder-birch-cottonwood-spruce (Tree) |
| Open Birch                          | Alder-birch-cottonwood-spruce (Tree) |
| Sparse/Open Cottonwood              | Alder-birch-cottonwood-spruce (Tree) |
| Tall Willow                         | Tall Willow                          |
| Low Willow                          | Low Willow                           |
| Dwarf Shrub/Moss Wetlands           | Wetlands                             |
| Elymus Forb                         | Wetlands                             |
| Elymus Grasslands                   | Wetlands                             |
| Ericaceous/Lichen Bog               | Wetlands                             |
| Graminoid Wetland                   | Wetlands                             |
| Low Willow-Wet                      | Wetlands                             |
| Myrica Gale Wetlands                | Wetlands                             |
| Myrica Gale/Dwarf Birch Wetlands    | Wetlands                             |
| Sedge Marsh                         | Wetlands                             |

*Table 4.3: cont'd*

| <b>Original Landcover Class</b> | <b>Analysis Landcover Class</b>      |
|---------------------------------|--------------------------------------|
| Sedge/Moss Wetlands             | Wetlands                             |
| Fern Forb Meadow                | Meadows                              |
| Fireweed Forb Meadow            | Meadows                              |
| Forb Meadow Mix                 | Meadows                              |
| Grass Forb Meadow               | Meadows                              |
| Mixed Grasslands                | Meadows                              |
| Heath/Dogwood                   | Meadows                              |
| Heath w/ Lichen                 | Lowland tundra                       |
| Heath Hummocks                  | Lowland tundra                       |
| Heath Hummocks w/ Forbs         | Lowland tundra                       |
| Heath w/ Forbs                  | Lowland tundra                       |
| Mud Flats                       | Lowland bare                         |
| Sand and Gravel - Beaches       | Lowland bare                         |
| Sand and Gravel - River Bars    | Lowland bare                         |
| Sand and Gravel - Roads         | Lowland bare                         |
| Dense Sitka Spruce              | Alder-birch-cottonwood-spruce (Tree) |
| Open Sitka Spruce               | Alder-birch-cottonwood-spruce (Tree) |
| Sitka Spruce Krummholz          | Alder-birch-cottonwood-spruce (Tree) |
| Sitka Spruce Regeneration       | Alder-birch-cottonwood-spruce (Tree) |



**Table 4.4:** Top 10 candidate subset models for three behavioral states aggregated. Variables in the top model for each variable subset were retained for final model selection.

| Model  | Model fit statistics <sup>a</sup> |              |       |
|--|-----------------------------------|--------------|-------|
|  | <i>K</i>                          | $\Delta$ AIC | $w_i$ |
| <b><i>Landcover</i></b>  |                                   |              |       |
| Cover + Elderberry salmonberry + Lowland tundra + Meadows                                | 5                                 | 0.00         | 1.00  |
| Dense alder + Elderberry salmonberry + Lowland tundra + Tree                             | 5                                 | 649.66       | 0.00  |
| Cover + Elderberry salmonberry + Lowland bare + Lowland tundra                           | 5                                 | 798.00       | 0.00  |
| Cover + Dense alder + Elderberry salmonberry + Lowland tundra                            | 5                                 | 917.78       | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Tall willow                            | 5                                 | 955.97       | 0.00  |
| Unique + Cover + Elderberry salmonberry + Lowland tundra                                 | 5                                 | 1369.04      | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Low willow                             | 5                                 | 1370.47      | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra  | 4                                 | 1378.36      | 0.00  |
| Dense alder + Elderberry salmonberry + Lowland tundra + Meadows                          | 5                                 | 2099.05      | 0.00  |
| Dense alder + Elderberry salmonberry + Meadows + Tree                                    | 5                                 | 2464.35      | 0.00  |
| <b><i>Edge Diversity</i></b>   |                                   |              |       |
| Elderberry salmonberry edge + Lowland tundra edge + Meadow edge + Tree edge              | 5                                 | 0.00         | 1.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Tree edge         | 5                                 | 168.04       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Meadow edge       | 5                                 | 486.76       | 0.00  |
| Elderberry salmonberry edge + Lowland bare edge + Lowland tundra edge + Tree edge        | 5                                 | 703.24       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Water edge        | 5                                 | 793.26       | 0.00  |
| Elderberry salmonberry edge + Lowland tundra edge + Tree edge + Water edge               | 5                                 | 795.72       | 0.00  |
| Elderberry salmonberry edge + Lowland tundra edge + Tall willow edge + Tree edge         | 5                                 | 877.35       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Tall willow edge  | 5                                 | 1016.62      | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland bare edge + Lowland tundra edge | 5                                 | 1077.34      | 0.00  |
| Elderberry salmonberry edge + Lowland tundra edge + Low willow edge + Tree edge          | 5                                 | 1320.79      | 0.00  |

Table 4.4: cont'd

| Model                       | Model fit statistics <sup>a</sup> |              |       |
|-----------------------------|-----------------------------------|--------------|-------|
|                             | <i>K</i>                          | $\Delta$ AIC | $w_i$ |
| <b><i>Topography</i></b>    |                                   |              |       |
| Elevation + TPI + TRI       | 4                                 | 0.00         | 1.00  |
| TPI + TRI                   | 3                                 | 135.38       | 0.00  |
| Elevation + Roughness + TPI | 4                                 | 186.43       | 0.00  |
| Elevation + Slope + TPI     | 4                                 | 328.20       | 0.00  |
| Roughness + TPI             | 3                                 | 361.38       | 0.00  |
| Slope + TPI                 | 3                                 | 502.46       | 0.00  |
| Elevation + TPI             | 3                                 | 2405.62      | 0.00  |
| Elevation + TRI             | 3                                 | 4003.49      | 0.00  |
| TRI                         | 2                                 | 4026.89      | 0.00  |
| Elevation + Roughness       | 3                                 | 4160.84      | 0.00  |

<sup>a</sup>Number of parameters (*K*), change in Akaike's Information Criterion score from the top model ( $\Delta$ AIC) and Akaike weights ( $w_i$ ).

**Table 4.5:** Top 10 candidate subset models for resting behavioral state. Variables in the top model for each variable subset were retained for final model selection.

| Model  | Model fit statistics <sup>a</sup> |              |       |
|--|-----------------------------------|--------------|-------|
|  | K                                 | $\Delta AIC$ | $w_i$ |
| <b><i>Landcover</i></b>  |                                   |              |       |
| Dense alder + Elderberry salmonberry + Lowland tundra + Tree                             | 5                                 | 0.00         | 1.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Meadows                                | 5                                 | 75.71        | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Tall willow                            | 5                                 | 141.30       | 0.00  |
| Cover + Dense alder + Elderberry salmonberry + Lowland tundra                            | 5                                 | 158.11       | 0.00  |
| Cover + Elderberry salmonberry + Lowland bare + Lowland tundra                           | 5                                 | 210.10       | 0.00  |
| Dense alder + Elderberry salmonberry + Lowland tundra + Meadows                          | 5                                 | 255.38       | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Low willow                             | 5                                 | 347.39       | 0.00  |
| Unique + Cover + Elderberry salmonberry + Lowland tundra                                 | 5                                 | 356.61       | 0.00  |
| Unique + Dense alder + Lowland tundra + Tree   | 5                                 | 410.82       | 0.00  |
| Dense alder + Lowland tundra + Meadows + Tree  | 5                                 | 412.17       | 0.00  |
| <b><i>Edge Diversity</i></b>   |                                   |              |       |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Meadow edge       | 5                                 | 0.00         | 1.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Tall willow edge  | 5                                 | 65.55        | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland bare edge + Lowland tundra edge | 5                                 | 164.03       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Low willow edge   | 5                                 | 247.72       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Tree edge         | 5                                 | 355.86       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge                     | 4                                 | 365.37       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Water edge        | 5                                 | 367.35       | 0.00  |
| Dense alder edge + Lowland bare edge + Lowland tundra edge + Meadow edge                 | 5                                 | 430.12       | 0.00  |
| Dense alder edge + Lowland tundra edge + Meadow edge + Tall willow edge                  | 5                                 | 493.16       | 0.00  |
| Dense alder edge + Lowland tundra edge + Low willow edge + Meadow edge                   | 5                                 | 550.95       | 0.00  |

Table 4.5: cont'd

| Model                       | Model fit statistics <sup>a</sup> |              |       |
|-----------------------------|-----------------------------------|--------------|-------|
|                             | <i>K</i>                          | $\Delta$ AIC | $w_i$ |
| <b><i>Topography</i></b>    |                                   |              |       |
| Elevation + TPI + TRI       | 4                                 | 0.00         | 1.00  |
| TPI + TRI                   | 3                                 | 11.49        | 0.00  |
| Elevation + Roughness + TPI | 4                                 | 73.73        | 0.00  |
| Roughness + TPI             | 3                                 | 92.28        | 0.00  |
| Elevation + Slope + TPI     | 4                                 | 137.94       | 0.00  |
| Slope + TPI                 | 3                                 | 154.87       | 0.00  |
| Elevation + TRI             | 3                                 | 716.36       | 0.00  |
| TRI                         | 2                                 | 735.74       | 0.00  |
| Elevation + Roughness       | 3                                 | 775.59       | 0.00  |
| Roughness                   | 2                                 | 787.75       | 0.00  |

<sup>a</sup>Number of parameters (*K*), change in Akaike's Information Criterion score from the top model ( $\Delta$ AIC) and Akaike weights ( $w_i$ ).

**Table 4.6:** Top 10 candidate subset models for foraging behavioral state. Variables in the top model for each variable subset were retained for final model selection.

| Model   | Model fit statistics |              |       |
|---|----------------------|--------------|-------|
|   | <i>K</i>             | $\Delta$ AIC | $w_i$ |
| <b><i>Landcover</i></b>   |                      |              |       |
| Cover + Elderberry salmonberry + Lowland tundra + Meadows                           | 5                    | 0.00         | 1.00  |
| Cover + Elderberry salmonberry + Lowland bare + Lowland tundra                      | 5                    | 376.65       | 0.00  |
| Dense alder + Elderberry salmonberry + Lowland tundra + Tree                        | 5                    | 398.50       | 0.00  |
| Cover + Dense alder + Elderberry salmonberry + Lowland tundra                       | 5                    | 463.39       | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Tall willow                       | 5                    | 562.27       | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Tree                              | 5                    | 610.54       | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra                                     | 4                    | 706.45       | 0.00  |
| Unique + Cover + Elderberry salmonberry + Lowland tundra                            | 5                    | 707.43       | 0.00  |
| Cover + Elderberry salmonberry + Lowland tundra + Low willow                        | 5                    | 707.95       | 0.00  |
| Dense alder + Elderberry salmonberry + Lowland tundra + Meadows                     | 5                    | 1074.51      | 0.00  |
| <b><i>Edge Diversity</i></b>  |                      |              |       |
| Elderberry salmonberry edge + Lowland tundra edge + Meadow edge + Tree edge         | 5                    | 0.00         | 1.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Tree edge    | 5                    | 289.01       | 0.00  |
| Elderberry salmonberry edge + Lowland bare edge + Lowland tundra edge + Tree edge   | 5                    | 325.20       | 0.00  |
| Elderberry salmonberry edge + Lowland tundra edge + Tree edge + Water edge          | 5                    | 364.55       | 0.00  |
| Elderberry salmonberry edge + Lowland tundra edge + Tall willow edge + Tree edge    | 5                    | 562.11       | 0.00  |
| Dense alder + Elderberry salmonberry + Lowland tundra + Meadow                      | 5                    | 572.85       | 0.00  |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Water edge   | 5                    | 673.98       | 0.00  |
| Elderberry salmonberry edge + Lowland tundra edge + Tree edge                       | 4                    | 705.37       | 0.00  |
| Elderberry salmonberry edge + Lowland tundra edge + Low willow edge + Tree edge     | 5                    | 707.37       | 0.00  |
| Dense alder + Elderberry salmonberry edge + Lowland bare edge + Lowland tundra edge | 5                    | 855.45       | 0.00  |
| <b><i>Topography</i></b>  |                      |              |       |
| Elevation + TPI + TRI   | 4                    | 0.00         | 1.00  |
| TPI + TRI   | 3                    | 77.02        | 0.00  |
| Elevation + Roughness + TPI   | 4                    | 128.62       | 0.00  |
| Elevation + Slope + TPI   | 4                    | 195.70       | 0.00  |
| Roughness + TPI   | 3                    | 232.23       | 0.00  |
| Slope + TPI   | 3                    | 297.07       | 0.00  |
| Elevation + TPI   | 3                    | 1306.00      | 0.00  |
| TPI   | 2                    | 2787.96      | 0.00  |
| Elevation + TRI   | 3                    | 2810.25      | 0.00  |
| TRI   | 2                    | 2827.88      | 0.00  |

**Table 4.7:** Top 10 candidate subset models for travel behavioral state.

| <b>Model</b>  | <b>Model fit statistics<sup>a</sup></b> |             |                      |
|---|---|-------------|----------------------|
|   | <b>K</b>                                | <b>ΔAIC</b> | <b>w<sub>i</sub></b> |
| <b><u>Landcover</u></b>   |   |             |                      |
| Cover + Elderberry salmonberry + Lowland tundra + Meadows                         | 5                                       | 0.0         | 1.00                 |
| Cover + Elderberry salmonberry + Lowland bare + Lowland tundra                    | 5                                       | 196.28      | 0.00                 |
| Cover + Elderberry salmonberry + Lowland tundra + Tall willow                     | 5                                       | 219.65      | 0.00                 |
| Dense alder + Elderberry salmonberry + Lowland tundra + Tree                      | 5                                       | 230.77      | 0.00                 |
| Unique + Cover + Elderberry salmonberry + Lowland tundra                          | 5                                       | 233.51      | 0.00                 |
| Cover + Dense alder + Elderberry salmonberry + Lowland tundra                     | 5                                       | 260.03      | 0.00                 |
| Cover + Elderberry salmonberry + Lowland tundra + Low willow                      | 5                                       | 261.87      | 0.00                 |
| Cover + Elderberry salmonberry + Lowland tundra                                   | 4                                       | 268.57      | 0.00                 |
| Cover + Elderberry salmonberry + Lowland tundra + Tree                            | 5                                       | 270.43      | 0.00                 |
| Cover + Elderberry salmonberry + Lowland bare + Meadows                           | 5                                       | 516.38      | 0.00                 |
| <b><u>Edge Diversity</u></b>  |   |             |                      |
| Elderberry salmonberry edge + Lowland tundra edge + Tree edge + Water edge        | 5                                       | 0.00        | 1.00                 |
| Elderberry salmonberry edge + Lowland tundra edge + Meadow edge + Tree edge       | 5                                       | 162.70      | 0.00                 |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Tree edge  | 5                                       | 200.11      | 0.00                 |
| Elderberry salmonberry edge + Lowland bare edge + Lowland tundra edge + Tree edge | 5                                       | 283.51      | 0.00                 |
| Elderberry salmonberry edge + Lowland tundra edge + Tall willow edge + Tree edge  | 5                                       | 284.32      | 0.00                 |
| Elderberry salmonberry edge + Lowland tundra edge + Low willow edge + Tree edge   | 5                                       | 325.82      | 0.00                 |
| Elderberry salmonberry edge + Lowland tundra edge + Tree edge                     | 4                                       | 345.71      | 0.00                 |
| Elderberry salmonberry edge + Meadow edge + Tree edge + Water edge                | 5                                       | 370.47      | 0.00                 |
| Dense alder edge + Elderberry salmonberry edge + Lowland tundra edge + Water edge | 5                                       | 559.05      | 0.00                 |
| Dense alder edge + Elderberry salmonberry edge + Meadow edge + Tree edge          | 5                                       | 643.32      | 0.00                 |
| <b><u>Topography</u></b>  |   |             |                      |
| Elevation + TPI + TRI   | 4                                       | 0.00        | 0.98                 |
| Elevation + Roughness + TPI   | 4                                       | 8.29        | 0.02                 |
| Elevation + Slope + TPI   | 4                                       | 15.39       | 0.00                 |
| TPI + TRI   | 3                                       | 57.39       | 0.00                 |
| Roughness + TPI   | 3                                       | 71.97       | 0.00                 |
| Elevation + TPI   | 3                                       | 77.00       | 0.00                 |
| Slope + TPI   | 3                                       | 79.88       | 0.00                 |
| TPI   | 2                                       | 361.11      | 0.00                 |
| TRI   | 2                                       | 664.51      | 0.00                 |
| Elevation + TRI   | 3                                       | 665.00      | 0.00                 |

**Table 4.8:** 5-fold cross validation results from female brown bear resource selection models, May through June. We considered models good predictors of resource selection when they had a high coefficient of determination, and 95% confidence intervals (CI) surrounding slope estimates ( $B_1$ ) that excluded zero and included 1. RSF models were considered acceptable when slope estimates excluded both zero and 1. Without NDVI.

| <b>K</b>                            | <b><math>r^2</math></b> | <b><math>B_0</math></b> | <b>CI</b>         | <b><math>B_1</math></b> | <b>CI</b>         |
|-------------------------------------|-------------------------|-------------------------|-------------------|-------------------------|-------------------|
| <b><i>All behavioral states</i></b> |                         |                         |                   |                         |                   |
| 1                                   | 0.97                    | -526.65                 | (-1116.64, 63.34) | 1.41                    | (1.06, 1.76)      |
| 2                                   | 0.97                    | 183.61                  | (-102.38, 469.59) | 0.83                    | (0.62, 1.03)      |
| 3                                   | 0.97                    | -58.62                  | (-419.83, 302.58) | 1.05                    | (0.80, 1.31)      |
| 4                                   | 0.95                    | -24.11                  | (-465.24, 417.03) | 1.02                    | (0.70, 1.34)      |
| 5                                   | 0.99                    | -339.62                 | (-670.04, -9.19)  | 1.25                    | (1.06, 1.44)      |
| <b><i>Resting</i></b>               |                         |                         |                   |                         |                   |
| 1                                   | 0.97                    | 31.95                   | (-30.56, 94.45)   | 0.86                    | (-30.56, 94.45)   |
| 2                                   | 0.99                    | -5.43                   | (-69.58, 58.72)   | 1.02                    | (-69.58, 58.72)   |
| 3                                   | 0.95                    | -94.18                  | (-291.21, 102.85) | 1.28                    | (-291.21, 102.85) |
| 4                                   | 0.99                    | 11.83                   | (-37.62, 61.29)   | 0.95                    | (-37.62, 61.29)   |
| 5                                   | 0.87                    | 10.28                   | (-215.98, 236.54) | 0.97                    | (-215.98, 236.54) |
| <b><i>Foraging</i></b>              |                         |                         |                   |                         |                   |
| 1                                   | 0.97                    | 66.46                   | (-73.45, 206.38)  | 0.87                    | (0.67, 1.06)      |
| 2                                   | 0.99                    | -96.26                  | (-232.81, 40.29)  | 1.17                    | (1.00, 1.33)      |
| 3                                   | 0.97                    | -181.69                 | (-476.03, 112.65) | 1.29                    | (0.96, 1.61)      |
| 4                                   | 0.98                    | 140.92                  | (39.50, 242.34)   | 0.72                    | (0.58, 0.87)      |
| 5                                   | 0.98                    | -145.59                 | (-336.82, 45.63)  | 1.27                    | (1.02, 1.52)      |
| <b><i>Traveling</i></b>             |                         |                         |                   |                         |                   |
| 1                                   | 0.96                    | -7.85                   | (-113.08, 97.37)  | 1.03                    | (0.72, 1.33)      |
| 2                                   | 0.95                    | -0.62                   | (-156.34, 155.34) | 1.00                    | (0.70, 1.30)      |
| 3                                   | 0.79                    | -53.64                  | (-323.05, 215.78) | 1.20                    | (0.35, 2.06)      |
| 4                                   | 0.92                    | -14.12                  | (-155.95, 127.72) | 1.05                    | (0.63, 1.47)      |
| 5                                   | 0.97                    | -179.55                 | (-366.21, 7.11)   | 1.41                    | (1.05, 1.76)      |

**Table 4.9:** 5-fold cross validation results from female brown bear resource selection models, May through June. We considered models good predictors of resource selection when they had a high coefficient of determination, and 95% confidence intervals (CI) surrounding slope estimates ( $B_1$ ) that excluded zero and included 1. RSF models were considered acceptable when slope estimates excluded both zero and 1. NDVI was included in these models.

| <b>K</b>                            | <b><math>r^2</math></b> | <b><math>B_0</math></b> | <b>CI</b>         | <b><math>B_1</math></b> | <b>CI</b>    |
|-------------------------------------|-------------------------|-------------------------|-------------------|-------------------------|--------------|
| <b><u>All behavioral states</u></b> |                         |                         |                   |                         |              |
| 1                                   | 0.96                    | 247.39                  | (-32.51, 527.29)  | 0.75                    | (0.54, 0.96) |
| 2                                   | 0.99                    | -115.70                 | (-339.34, 107.93) | 1.12                    | (0.95, 1.29) |
| 3                                   | 0.98                    | -12.77                  | (-377.89, 352.36) | 1.01                    | (0.81, 1.21) |
| 4                                   | 0.96                    | -164.87                 | (-615.37, 285.64) | 1.16                    | (0.84, 1.48) |
| 5                                   | 0.98                    | -314.99                 | (-870.56, 240.57) | 1.21                    | (0.94, 1.47) |
| <b><u>Resting</u></b>               |                         |                         |                   |                         |              |
| 1                                   | 0.99                    | -30.22                  | (-140.74, 80.30)  | 1.06                    | (0.90, 1.22) |
| 2                                   | 0.94                    | -46.22                  | (-187.55, 95.11)  | 1.19                    | (0.78, 1.60) |
| 3                                   | 0.96                    | -86.56                  | (-199.99, 26.86)  | 1.41                    | (1.03, 1.79) |
| 4                                   | 0.94                    | 34.78                   | (-50.02, 119.58)  | 0.83                    | (0.55, 1.12) |
| 5                                   | 0.98                    | -30.57                  | (-120.13, 59.00)  | 1.11                    | (0.88, 1.35) |
| <b><u>Foraging</u></b>              |                         |                         |                   |                         |              |
| 1                                   | 0.98                    | -28.80                  | (-210.56, 152.95) | 1.05                    | (0.82, 1.28) |
| 2                                   | 0.95                    | 64.88                   | (-75.87, 205.63)  | 0.83                    | (0.55, 1.09) |
| 3                                   | 0.99                    | -42.32                  | (-182.71, 98.06)  | 1.07                    | (0.91, 1.22) |
| 4                                   | 0.98                    | -154.98                 | (-362.44, 52.48)  | 1.24                    | (1.01, 1.46) |
| 5                                   | 0.99                    | -65.79                  | (-165.16, 33.59)  | 1.12                    | (0.99, 1.24) |
| <b><u>Traveling</u></b>             |                         |                         |                   |                         |              |
| 1                                   | 0.94                    | -52.46                  | (-208.11, 103.18) | 1.17                    | (0.76, 1.57) |
| 2                                   | 0.94                    | -53.46                  | (-219.72, 112.81) | 1.16                    | (0.75, 1.56) |
| 3                                   | 0.97                    | -70.76                  | (-205.89, 64.36)  | 1.20                    | (0.88, 1.52) |
| 4                                   | 0.94                    | 34.95                   | (-68.93, 138.82)  | 0.87                    | (0.55, 1.19) |
| 5                                   | 0.93                    | -130.84                 | (-382.64, 120.95) | 1.32                    | (0.81, 1.82) |



**Table 4.10:** Parameter estimates with 95% confidence intervals for predictor variables in models describing female brown bear resource selection during the post denning period.

| Parameter                           | Estimate | SE    | 95% CI |       |
|-------------------------------------|----------|-------|--------|-------|
|                                     |          |       | Lower  | Upper |
| <b><i>All behavioral states</i></b> |          |       |        |       |
| Cover                               | 0.50     | 0.01  | 0.48   | 0.51  |
| Elderberry                          | -0.60    | 0.01  | -0.62  | -0.58 |
| Lowland tundra                      | -0.43    | 0.02  | -0.46  | -0.40 |
| Meadows                             | -0.23    | 0.01  | -0.25  | -0.21 |
| Elevation                           | 0.10     | 0.01  | 0.07   | 0.12  |
| TPI                                 | -0.23    | 0.01  | -0.25  | -0.22 |
| TRI                                 | 0.41     | 0.01  | 0.40   | 0.43  |
| Stream length                       | 0.19     | 0.003 | 0.18   | 0.19  |
| <b><i>Resting</i></b>               |          |       |        |       |
| Dense alder                         | 0.53     | 0.01  | 0.50   | 0.55  |
| Elderberry<br>salmonberry           | -0.37    | 0.02  | -0.40  | -0.34 |
| Tree                                | 0.47     | 0.01  | 0.44   | 0.49  |
| Lowland tundra edge                 | -0.41    | 0.04  | -0.48  | -0.34 |
| Elevation                           | 0.29     | 0.02  | 0.24   | 0.33  |
| TPI                                 | -0.16    | 0.02  | -0.19  | -0.14 |
| TRI                                 | 0.56     | 0.02  | 0.53   | 0.60  |
| Stream length                       | 0.14     | 0.01  | 0.13   | 0.16  |
| <b><i>Foraging</i></b>              |          |       |        |       |
| Cover                               | 0.47     | 0.01  | 0.45   | 0.49  |
| Elderberry<br>salmonberry           | -0.70    | 0.02  | -0.73  | -0.67 |
| Meadows                             | -0.66    | 0.03  | -0.72  | -0.59 |
| Lowland tundra edge                 | -0.58    | 0.02  | -0.62  | -0.54 |
| Meadows edge                        | 0.39     | 0.03  | 0.33   | 0.44  |
| TPI                                 | -0.31    | 0.01  | -0.33  | -0.29 |
| TRI                                 | 0.51     | 0.01  | 0.49   | 0.53  |
| Stream length                       | 0.21     | 0.01  | 0.20   | 0.22  |
| <b><i>Traveling</i></b>             |          |       |        |       |
| Cover                               | 0.52     | 0.02  | 0.49   | 0.55  |
| Elderberry<br>salmonberry           | -0.44    | 0.02  | -0.47  | -0.40 |
| Lowland tundra                      | -0.21    | 0.02  | -0.25  | -0.16 |
| Tree edge                           | 0.15     | 0.01  | 0.12   | 0.17  |
| Water edge                          | 0.26     | 0.01  | 0.24   | 0.29  |
| Elevation                           | 0.43     | 0.01  | 0.40   | 0.46  |
| TPI                                 | -0.14    | 0.01  | -0.17  | -0.12 |
| Stream length                       | 0.07     | 0.01  | 0.06   | 0.09  |

**Table 4.11:** Parameter estimates with 95% confidence intervals for predictor variables in models describing female brown bear resource selection during the post denning period, 15 May through 30 June. These Models included the NDVI covariate.

| Parameter                           | 95% CI   |       |       |       |
|-------------------------------------|----------|-------|-------|-------|
|                                     | Estimate | SE    | Lower | Upper |
| <b><i>All behavioral states</i></b> |          |       |       |       |
| Cover                               | 0.44     | 0.01  | 0.43  | 0.46  |
| Elderberry salmonberry              | -0.62    | 0.01  | -0.65 | -0.60 |
| Lowland tundra                      | -0.45    | 0.02  | -0.48 | -0.42 |
| Meadows                             | -0.26    | 0.01  | -0.28 | -0.24 |
| Elevation                           | 0.17     | 0.01  | 0.15  | 0.19  |
| TPI                                 | -0.25    | 0.01  | -0.26 | -0.24 |
| TRI                                 | 0.41     | 0.01  | 0.39  | 0.43  |
| Stream length                       | 0.19     | 0.004 | 0.18  | 0.19  |
| NDVI                                | 0.20     | 0.01  | 0.19  | 0.22  |
| <b><i>Resting</i></b>               |          |       |       |       |
| Dense alder                         | 0.50     | 0.01  | 0.48  | 0.52  |
| Elderberry salmonberry              | -0.39    | 0.02  | -0.42 | -0.36 |
| Tree                                | 0.45     | 0.01  | 0.42  | 0.47  |
| Lowland tundra edge                 | -0.43    | 0.04  | -0.51 | -0.36 |
| Elevation                           | 0.41     | 0.02  | 0.37  | 0.46  |
| TPI                                 | -0.18    | 0.01  | -0.20 | -0.16 |
| TRI                                 | 0.55     | 0.02  | 0.52  | 0.59  |
| Stream length                       | 0.14     | 0.01  | 0.13  | 0.16  |
| NDVI                                | 0.25     | 0.02  | 0.22  | 0.28  |
| <b><i>Foraging</i></b>              |          |       |       |       |
| Cover                               | 0.38     | 0.01  | 0.36  | 0.40  |
| Elderberry salmonberry              | -0.75    | 0.02  | -0.78 | -0.71 |
| Meadows                             | -0.67    | 0.03  | -0.74 | -0.61 |
| Lowland tundra edge                 | -0.63    | 0.02  | -0.67 | -0.59 |
| Meadows edge                        | 0.34     | 0.03  | 0.29  | 0.39  |
| TPI                                 | -0.32    | 0.01  | -0.34 | -0.30 |
| TRI                                 | 0.54     | 0.01  | 0.52  | 0.56  |
| Stream length                       | 0.20     | 0.01  | 0.19  | 0.22  |
| NDVI                                | 0.22     | 0.01  | 0.20  | 0.24  |
| <b><i>Traveling</i></b>             |          |       |       |       |
| Cover                               | 0.51     | 0.02  | 0.48  | 0.54  |
| Elderberry salmonberry              | -0.44    | 0.02  | -0.48 | -0.41 |

*Table 11: cont'd*

| Parameter     | 95% CI   |      |       |       |
|---------------|----------|------|-------|-------|
|               | Estimate | SE   | Lower | Upper |
| Tree edge     | 0.14     | 0.01 | 0.11  | 0.17  |
| Water edge    | 0.27     | 0.01 | 0.25  | 0.30  |
| Elevation     | 0.48     | 0.02 | 0.45  | 0.51  |
| TPI           | -0.15    | 0.01 | -0.18 | -0.13 |
| Stream length | 0.07     | 0.01 | 0.06  | 0.08  |
| NDVI          | 0.10     | 0.01 | 0.08  | 0.13  |

<sup>1</sup>Includes dense alder, tall willow, and tree cover

**Table 4.12:** Models evaluating female brown bear resource selection from all behavioral states, and in stationary, foraging/loafing, and moving behaviors. Variables assessed in candidate models were from variable subset models that were retained for final model selection.

| Model  | Model fit statistics <sup>a</sup> |              |       |
|--|-----------------------------------|--------------|-------|
|  | <i>K</i>                          | $\Delta$ AIC | $w_i$ |
| <b><i>All behavioral states</i></b>  |                                   |              |       |
| Cover <sup>b</sup> + Elderberry Salmonberry + Lowland tundra + Meadows + Elevation + TPI + TRI + Stream length + NDVI          | 11                                | 0.00         | 1.00  |
| Cover <sup>b</sup> + Elderberry Salmonberry + Lowland tundra + Meadows + Elevation + TPI + TRI + Stream length                 | 10                                | 837.5        | 0.00  |
| <b><i>Resting</i></b>  |                                   |              |       |
| Dense alder + Elderberry Salmonberry + Tree + Lowland tundra edge + Elevation + TPI + TRI + Stream length + NDVI               | 11                                | 0.00         | 1.00  |
| Dense alder + Elderberry Salmonberry + Tree + Lowland tundra edge + Elevation + TPI + TRI + Stream length                      | 10                                | 274.75       | 0.00  |
| <b><i>Foraging</i></b>   |                                   |              |       |
| Cover <sup>b</sup> + Elderberry Salmonberry + Meadows + Lowland tundra edge + Meadows edge + TPI + TRI + Stream length + NDVI  | 11                                | 0.00         | 1.00  |
| Cover <sup>b</sup> + Elderberry Salmonberry + Meadows + Lowland tundra edge + Meadows edge + TPI + TRI + Stream length         | 10                                | 481.95       | 0.00  |
| <b><i>Traveling</i></b>  |                                   |              |       |
| Cover <sup>b</sup> + Elderberry Salmonberry + Lowland tundra + Tree edge + Water edge + Elevation + TPI + Stream length + NDVI | 11                                | 0.00         | 1.00  |
| Cover <sup>b</sup> + Elderberry Salmonberry + Lowland tundra + Tree edge + Water edge + Elevation + TPI + Stream length        | 10                                | 71.29        | 0.00  |

<sup>a</sup>Number of parameters (*K*), change in Akaike's Information Criterion score from the top model ( $\Delta$ AIC) and Akaike weights ( $w_i$ ).

<sup>b</sup>Includes dense alder, tall willow and tree land cover

**Table 4.13:** Comparison of RSF Models with NDVI.

| Parameter              | Parameter Estimate |                  |                   |                 |
|------------------------|--------------------|------------------|-------------------|-----------------|
|                        | All Behaviors      | Resting Behavior | Foraging Behavior | Travel Behavior |
| Cover                  | +0.44              | -                | +0.38             | +0.51           |
| Elderberry-Salmonberry | -0.62              | -0.39            | -0.75             | -0.44           |
| Dense Alder            | -                  | +0.50            | -                 | -               |
| Tree                   | -                  | +0.45            | -                 | -               |
| Lowland Tundra         | -0.45              | -                | -                 | -0.21           |
| Meadows                | -0.26              | -                | -0.67             | -               |
| Lowland Tundra Edge    | -                  | -0.43            | -0.63             | -               |
| Meadows Edge           | -                  | -                | +0.34             | -               |
| Tree Edge              | -                  | -                | -                 | +0.14           |
| Water Edge             | -                  | -                | -                 | +0.27           |
| Elevation              | +0.17              | +0.41            | -                 | +0.48           |
| TPI                    | -0.25              | -0.18            | -0.32             | -0.15           |
| TRI                    | +0.55              | +0.55            | +0.54             | -               |
| Stream Length          | +0.19              | +0.14            | +0.20             | +0.07           |
| NDVI                   | +0.20              | +0.25            | +0.22             | +0.10           |

FIGURES

Figure 4.1: Kodiak Island, Alaska study area for Kodiak brown bear female movement during.

